Consequences of reduced bird densities for seed dispersal

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“The creation of a thousand forests is in one acorn”

-Ralph Waldo Emerson

Table of Contents

Abstract

The decline in range and density of frugivorous birds worldwide could have consequences for the functioning of ecosystem processes such as seed dispersal. I endeavoured to determine the effects of bird declines on seed dispersal and assess the current status of dispersal in New Zealand. My first aim was to determine whether decreased bird density can reduce competitive interactions between birds, leading to birds concentrating on higher-reward fruit species. I measured fruit removal rates and fruit preferences of birds in Canterbury forest remnants with high (Hay and Prices) and low (Lords and Kaituna) bird densities. Removal rates of *Melicytus ramiflorus* and *Coprosma* spp. were lower at low-bird sites, and the size of this effect was greater for low-reward plant species. *Coprosma areolata* (a low-sugar fruit) had limited dispersal at Kaituna (59% fruit removed by end of 2012 season), compared with 92% removal at Hay, whereas 99-100% of *M. ramiflorus* and *C. robusta* (higher-sugar) fruits were removed at both sites. My second aim was to determine whether seed dispersal by introduced possums (*Trichosurus vulpecula*) can compensate for bird declines. I analysed seeds present in possum and bird faecal samples collected at Kowhai Bush, Kaikoura. Possums dispersed <3% of the total seeds, much less than bellbirds (21%), silvereyes (16%), song thrushes (33%) and blackbirds (28%). Possums also destroyed approximately 15% of seeds found in faeces, reduced the germination of gut-passed *C. robusta* seed to half of that from bird faeces (30% vs. 60-70%), and did not swallow fruits any larger than those moved by the much smaller birds (c. 7 mm diameter). My third aim was to determine the relationship between percentage of fruits dispersed and distance from parent tree for three large-seeded trees; *Beilschmiedia tawa*, *Elaeocarpus dentatus*, and *Prumnopitys ferruginea*. I fitted dispersal kernels to the observed dispersal distances out to 50 m for both undispersed whole fruits and seeds consumed by a bird, and found that dispersal quantity below the parent tree strongly underestimates total dispersal quantity. The average percentage dispersed overall was 81% for *B. tawa*, 75% for *E. dentatus* and 91% for *P. ferruginea*, and for all species finding only 11-18% clean seeds under the parent tree would correspond to an overall percent dispersed of at least 50% of the whole seed crop. My final aim was to determine the consequences of dispersal failure for recruitment in three plant species; *Elaeocarpus hookerianus*, *Ripogonum scandens*, and *C. robusta*. I compared the fate of dispersed and undispersed seeds in a manipulative field experiment. Exclusion of mammals plus removal of fruit pulp had the greatest effect on survival, while the combined effects of dispersal failure (under parent, high density, whole fruit) and inclusion of mammals decreased the number of live seedlings present at the final count by 75-92%. Overall, most native plants were receiving adequate dispersal and there was little evidence for strong risks to plant regeneration from dispersal failure, despite the reduced bird densities and ongoing negative effects of introduced mammals in New Zealand.

Preface

The overall objective of this thesis is to investigate the effects of bird declines on seed dispersal in New Zealand and to evaluate the current status of this ecological process. I attempt to answer this broad question in four main data chapters. These chapters (2-5) have been written as stand-alone scientific papers that can be read independently. Consequently, there is a small amount of repetition between chapters in order to provide the relevant background to each. Except where noted below, all the experimental work, data analysis and writing in this thesis is my own.

Chapter 2 includes a fruit nutrient analysis conducted by NZ Labs, Auckland. Fruit pulp collection and preparation for the analysis was done by myself and Rocio Jana. Chapter 3 includes seed identifications, of which Colin Webb confirmed the identity of five species. The eight year *Beilschmiedia tawa* data set used in Chapter 4 was provided by Dave Kelly, while the *Elaeocarpus dentatus* and *Prumnopitys ferruginea* data sets were collected myself. Elena Moltchanova provided statistical advice and helped write the R and WinBUGS code used for this chapter. A manuscript entitled "Even the bad years are good: calibrating overall seed dispersal quantity against measurements under the parent canopy", which is based on Chapter 4, was submitted to the journal 'Ecology' on 23 May 2013. The version presented in this thesis is the version written myself before revisions were made by co-authors prior to journal submission.

All other data chapters are in preparation for submission to journals. Figures and tables are numbered within each chapter, while all references are provided at the end of the thesis to avoid repetition.

This research was carried out with animal ethics approval from the University of Canterbury Animal Ethics Committee (AEC Ref: 2012/10R) and a Low Impact Research and Collection Permit from the New Zealand Department of Conservation (National Permit Number: CA-5160-OTH). Additional permissions were obtained from QEII National Trust.

Chapter 1: Introduction

Seed dispersal in action: silvereye and *Coprosma* berry. Photo: R. South.

In the face of worldwide bird declines, there is considerable interest in how well bird-plant interactions are faring, especially fruit dispersal mutualisms. This is particularly so in New Zealand, with Jared Diamond famously commenting that New Zealand no longer has an avifauna, just the wreckage of one (Diamond 1984). Many New Zealand terrestrial bird species are extinct or declining (Holdaway 1989) putting at risk pollination and dispersal services (Robertson *et al.* 2008). This research will investigate an important ecological question: what are the effects of bird declines on the seed dispersal services they provide to plants?

Seed dispersal

Seed dispersal processes are essential for the persistence of plant populations. Successful seed dispersal consists of movement of seeds from a source tree to sites where seeds can germinate and seedlings can establish. Experimental and theoretical research suggests that the initial spatial distribution of dispersed seeds plays an important role in determining the structure and dynamics of plant populations and communities (Nathan & Muller-Landau 2000; Levine & Murrell 2003). The pattern of seed dispersal serves as a template for subsequent processes such as germination, predation, competition, and survival, all of which can ultimately affect the spatial distribution of adult plants (Schupp & Fuentes 1995). Seeds are dispersed by both biotic (e.g. animal) and abiotic (e.g. wind, water) dispersal agents. Animal dispersal can take place either externally through attachment of seeds to the animal's body, or internally through ingestion of seeds. If effective, internal animal-mediated seed dispersal can be mutualistic, whereby both plant and dispersing animal derive a benefit. Plants use nutritious fruits or similar structures to reward seed dispersing animals. The seeds are ingested incidentally by the animal disperser along with the pulp, then later defecated, regurgitated or spat out intact. Dispersal of fleshy-fruited plant species via ingestion by animals (endozoochory) is the focus of this thesis.

In most plant communities, birds and mammals are the main animal seed dispersers (Herrera 2002). Birds have many advantages as seed dispersers as they are widespread, highly mobile, can travel long distances, lack teeth, and typically swallow fruits and seeds intact (Whelan *et al.* 2008). The ecosystem services provided by seed dispersing birds include removal of seeds from the parent plant, escape from seed predators, improved germination, increased gene flow, and restoration of disturbed ecosystems (Sekercioglu *et al.* 2004).

The escape hypothesis, first proposed by Janzen (1970) and Connell (1971), posited that seed dispersal reduces density-dependent mortality of seeds and seedlings by allowing escape from competitors, seed predators, pathogens, and herbivores. Since seed density generally decreases

away from parent plants, seed dispersal can improve survival chances by reducing competition between seedlings (Herrera 2002). Herbivores and seed predators may concentrate on abundant food resources near the parent plant so that mortality increases with increasing density (Schupp 1992). The Janzen-Connell model is thought to maintain high tree diversity in tropical forests because natural enemies will reduce offspring density beneath parent trees, sometimes to zero, creating opportunities for heterospecific recruitment (Packer & Clay 2000). The model was not expected to hold in temperate forests due to higher abundances of natural enemies and a greater degree of natural enemy specialisation in aseasonal tropical habitats (Janzen 1970). Janzen and Connell theorized that the unpredictable fluctuations in the physical environment of temperate forests (such as weather changes) may cause fluctuations in seed or seedling predators, lifting the predation pressure from juvenile plants. As a result, few studies of Janzen-Connell effects have been conducted in temperate forests compared to very many studies in tropical forests. There is, however, an increasing number of studies showing that Janzen-Connell effects are in fact also important in temperate plant species (Packer & Clay 2000; Fitzsimons & Miller 2010; Martin & Canham 2010; Wotton & Kelly 2011). HilleRisLambers *et al.* (2002) found that the proportion of species affected by density-dependent mortality is equivalent in temperate and tropical forests.

Processing (or gut passage) of seeds by frugivores can enhance germination via three mechanisms: (1) the scarification effect: abrasion of the seed coat increases permeability of the coat to water and gases; (2) the deinhibition effect: removal of pulp and associated germination inhibitors from seeds; and (3) the fertilization effect: faecal material surrounding the seed enhances germination and seedling growth (Robertson *et al.* 2006). A meta-analysis on the scarification effect showed that ingested seeds germinate in greater numbers and take less time to germinate than hand-cleaned seeds (Traveset & Verdu 2002). However, most of the information used in the meta-analysis came from studies carried out in the laboratory, which may not reflect what happens in nature (Traveset *et al.* 2007). Glasshouse and field tests generally show that scarification makes little consistent difference to final germination percentage (Robertson *et al.* 2006; Traveset *et al.* 2007; Kelly *et al.* 2010). Until recently, the deinhibition effect has received less attention than the scarification effect, though studies by Burrows (1995c; 1995a; 1995d; 1995b; 1996a; 1996f; 1996e; 1996b; 1996c; 1996d; 1999b; 1999a) showed many New Zealand plant species failing to germinate from whole fruits. This raised concern that seeds would die before germinating if they were not ingested by a frugivore. Robertson *et al.* (2006) later found that germination of seeds in whole fruits was much higher in glasshouse and field experiments than in laboratory trials. The lack of germination in the laboratory was inferred to be an artefact of using Petri dishes, presumably preventing inhibitors to naturally leach away as they would in the field. The removal of fruit pulp,

although not as vital for germination as once thought, generally increases germination and is significantly greater than the more often studied scarification effect (Robertson *et al.* 2006). However, there is a crucial need to determine whether seeds that do not germinate from whole fruits are dead or alive (but dormant) (Kelly *et al.* 2004; Robertson *et al.* 2006). Most germination experiments are terminated after a few months and dormancy of seeds that did not germinate is unknown (Traveset 1998). If seeds in fruits are merely dormant, they may germinate later and a delay in germination may have no cost to the plant or may even serve as a conditional strategy for dispersal in time (Kelly *et al.* 2004). Studies on the fertilization effect are sparse, though there is evidence that manure can have a fertilizing effect on seedling growth (e.g. Traveset *et al.* 2001).

Plant meta-populations are spatially separated populations that are linked by immigration (seed dispersal) and gene flow (dispersal and pollination). The arrival of people to New Zealand brought about deforestation, agricultural land use, and urban development, reducing a once-continuous New Zealand forest cover in many places, to small scattered fragments (Meurk & Swaffield 2000). The extent to which these forest patches are linked by seed dispersal depends on the frequency of long-distance dispersal events. Plant meta-populations are often separated by hundreds of metres or more, while most seeds are dispersed less than 100 m (Cain *et al.* 2000). Because of the inherent difficulty of measuring long-distance seed dispersal, few data sets exist and we have little idea of how much is necessary for the maintenance of meta-populations (Kelly *et al.* 2010). Isolated fragments may be at risk of losing genetic diversity and potentially adaptive genetic variation (Sork & Smouse 2006). The genetic consequences of seed dispersal (and long-distance pollination) are largely unknown, although fragmented tree populations are particularly vulnerable to inbreeding depression (Scofield & Schultz 2006), and small plant population sizes in fragments may create genetic bottlenecks (Sork & Smouse 2006).

Seed dispersal allows plants to colonise new or disturbed habitats (Caves *et al.* 2013). Since favourable sites are unpredictable in space and time, dispersing seeds widely is advantageous so that some may encounter a favourable situation as it occurs (Howe & Smallwood 1982). Recruitment limitation is defined as "the failure to have any viable juveniles at an available site" (Hurtt & Pacala 1995 p.2). This limitation is thought to have important implications in the maintenance of plant diversity since a given plant may successfully establish in a given site simply because superior competitors have failed to do so, allowing rare and less competitive species to persist (Schupp *et al.* 2002). Although recruitment limitation may maintain species richness, it may also have "detrimental repercussions on the recruitment processes of plants if it is extended beyond a certain threshold" (Stoner & Henry 2008 p 12). This could be possible in New Zealand forests where native avian dispersers currently have low densities. Dispersal limitation may reach a maximum, disrupting

dispersal processes and precluding the reproduction and recolonisation of plants (Stoner & Henry 2008).

Effects of bird declines on dispersal

The vulnerability of a plant species to the loss of animal mutualists is increased by plant dependence on one or a few animal species (Bond 1994). While several different pollinators may service a plant, some degree of host specificity is usually required for effective pollination rates (Handel 1997). Plants require pollen to be moved to a conspecific flower and usually provide incentives at flowers which serve to attract suitable pollinators. Host-specificity is encouraged by a 'payment upon delivery' of the pollen. In contrast, frugivores must be 'paid in advance', making it more difficult for plants to direct seed dispersers to particular targets. Moreover, these targets (appropriate sites for germination and establishment) vary in space and time, and are difficult to specify or recognise. Consequently, animal-mediated seed dispersal is thought to be a more diffuse mutualism than pollination (Wheelwright & Orians 1982), where one frugivore typically feeds on many plant species and each fleshy-fruited plant species is fed on by multiple frugivores (Yoshikawa & Isagi 2012). Increasing specificity is associated with increasing fruit or seed size, especially for birds, whereby gape size limits the size of fruit a bird can swallow. For example, extinction of large-bodied frugivorous birds in southern Spain has left *Laurus nobilis* almost entirely dependent on one species (blackbirds, *Turdus merula*) for dispersal (Hampe 2003).

Even with relatively low host-specificity in dispersal systems, there is still cause for concern. Worldwide, there is evidence that reduced abundances of animal dispersers are negatively affecting dispersal. For example, reductions in frugivore abundance can decrease the dispersal service received by plants (Riera *et al.* 2002; Cordeiro & Howe 2003; Terborgh *et al.* 2008). This decreased dispersal can result in plant population declines (Christian 2001; Sharam *et al.* 2009; Traveset *et al.* 2012), and changes in species composition (McConkey *et al.* 2012). Some examples of systems where plant reproductive declines followed local extinction of mutualists are mammal-dispersed trees in Thailand and central Africa (Brodie *et al.* 2009; Vanthomme *et al.* 2010), and bird-dispersed plants in Australia and Hawaii (Moran *et al.* 2009; Chimera & Drake 2010). Island ecosystems are particularly vulnerable to avian extinctions (Olson 1989). Most isolated islands such as Hawaii, Mauritius, Madagascar and New Zealand have birds that evolved without mammalian predation and all have suffered from environmental change brought about by human colonisation in the last 800-1000 years (Diamond 1984; Gibbs 2006; Steadman 2006).

Seed dispersal in New Zealand

Seed plants are the most conspicuous element of the New Zealand flora (Wilton & Breitwieser 2000). The New Zealand native seed plant flora contains 1976 species in 105 families and 360 genera (Allan Herbarium 2000; Kelly *et al.* 2010). Fleshy fruits occur in 13% of all native vascular species and 59% of native tree species (Thorsen *et al.* 2009; Kelly *et al.* 2010). Due to geographic isolation, the New Zealand flora evolved with an unusual frugivore assemblage with almost no mammals (Lord *et al.* 2002). The fauna was instead dominated by birds (Holdaway 1989; Lee *et al.* 2010), with some fruit consumption by bats and lizards (Whitaker 1987; Lloyd 2001). The arrival of humans in New Zealand (ca. 1280 AD; Wilmshurst *et al.* 2008), and introduction of mammalian predators, had a devastating impact on the native fauna. Several species were hunted to extinction, most notably the nine species of moa (Dinornithiformes), plus others such as huia (*Heteralocha acutirostris*) and adzebill (*Aptornis otidiformis*) (Holdaway 1999; Tennyson 2010). The most damage, however, was caused by habitat destruction and introduced mammals that preyed on or competed with native species, particularly rats (the Polynesian rat or kiore (*Rattus exulans*) introduced by Maori and the Norway rat (*R. norvegicus*) and ship rat (*R. rattus*) subsequently introduced by Europeans), but also stoats (*Mustela erminea*), weasels (*M. nivalis*), ferrets (*M. furo*), cats (*Felis catus*), mice (*Mus musculus*), and possums (*Trichosurus vulpecula*) (O'Donnell 1996; Innes *et al.* 2010). Approximately 24% of land birds and 41% of forest birds are now extinct (Tennyson 2010). About half a dozen of these extinct birds were frugivores such as moa, huia, and piopio (*Turnagra* sp.) (Clout & Hay 1989). Other frugivorous birds are now uncommon or range-restricted, for example, kokako (*Callaeas cinerea*), hihi (*Notiomystis cincta*) and saddlebacks (*Philesturnus carunculatus*) persist only in small isolated sanctuaries (Robertson *et al.* 2007).

As well as introducing mammalian predators that caused bird species extinctions and declines, humans also brought with them 38 exotic bird species that established successfully, introduced primarily by acclimatisation societies (Duncan 1997). Of these, three are important seed dispersers in their native countries and are now widespread in New Zealand: blackbird (*Turdus merula*), song thrush (*Turdus philomelos*) and starling (*Sturnus vulgaris*). Although these introduced birds visit fruits, and are widespread and abundant, their effectiveness as dispersers of native fruits is still uncertain. Kelly *et al.* (2006) list 22 bird species (15 native and seven introduced) as current fruit visitors, however, the vast majority (84%) of visits to native fleshy fruits in their study were made by four native birds; silvereyes (*Zosterops lateralis*), bellbirds (*Anthornis melanura*), tui (*Prosthemadera novaeseelandiae*) and kereru (New Zealand pigeons, *Hemiphaga novaeseelandiae*). Consequently, dispersal of native fleshy fruits is thought to be largely dependent on these four native birds (Kelly *et*

al. 2006). All of these birds except silvereyes (self-introduced from Australia in 1856; Heather & Robertson 2000) have been reduced in density and/or range. There is particular concern for dispersal of the largest-seeded tree species (fruit width greater than 14 mm), which is now mainly dependent on a single large frugivore, the kereru (Kelly *et al.* 2010). Kereru have suffered serious population declines since human settlement, though their numbers are slowly increasing and they are now listed as not threatened, though conservation-dependent (Miskelly *et al.* 2008).

There is evidence that the loss of bird mutualists in New Zealand can affect plant reproduction (Kelly *et al.* 2006). There have been mainland-island comparisons showing that fruit dispersal is reduced or slowed (i.e. a higher proportion of ripe or overripe fruit) on the mainland compared to offshore islands where bird numbers are higher. These studies suggest that the fruit dispersal of *Fuchsia excorticata* (tree fuchsia), *Rhopalostylis sapida* (nikau), and *Pittosporum crassifolium* (karo) is reduced or slowed by a lack of frugivores on the mainland (McNutt 1998; Anderson *et al.* 2006; Robertson *et al.* 2008).

Since the occurrence of these native bird declines plus the introduction of exotic birds and mammals, plant-frugivore relationships are likely to have undergone major changes (Holdaway 1989; Lee *et al.* 1991; Thorsen *et al.* 2009). These changes have implications for plants that rely on native birds for seed dispersal. Introduced mammals as well as birds may consume fruits, contributing to seed dispersal, but their role in New Zealand has been given little attention until recently. Consequently, there is considerable scope to study the potential impacts of the loss of native birds and the replacement by exotic birds and mammals on ecosystem processes such as seed dispersal.

Thesis outline

The overall objective of this thesis is to determine the effects of bird declines on seed dispersal and to evaluate the current status of this ecological process in New Zealand. I attempt to answer this broad question by focusing on four aspects, covering different stages of the seed dispersal process and using different methods of measuring seed dispersal.

In Chapter 2, I begin by comparing fruit removal rates and fruit preferences of birds at sites with high and low bird densities, to determine whether bird density can alter competitive interactions between birds and lead to changes in diet choice. This has implications for plants that require seed dispersal services from birds and could lead to differential selection against certain plant species, resulting in a decline of those species.

In Chapter 3, I compare the seed dispersal of birds and introduced possums by analysing seeds present in faecal samples, to determine whether possum seed dispersal can compensate for bird declines. Possums are known to include fruit in their diet, however, little is known regarding possum seed dispersal quantity and quality compared to that of birds. I estimate the total contribution to seed dispersal by birds and possums by combining estimates of the number of seeds dispersed and the relative abundance of each species per hectare.

In Chapter 4, I investigate the relationship between the percentage of fruit dispersed and distance from parent tree for three large-seeded tree species. I use Bayesian statistics to fit 2Dt dispersal kernels to the observed dispersal distances for both undispersed whole fruits and seeds consumed by a bird. The results allow the percent through-bird at various distances from the parent tree to be determined, and an overall estimate of dispersal service (out to a 50 m radius around the tree).

In Chapter 5, I investigate the consequences of dispersal failure and mammalian predation on early plant recruitment, by comparing the fate of dispersed and undispersed seeds for three plant species in a manipulative field experiment. Specifically, I examine whether post-dispersal seed predation, germination, or seedling survival is affected by movement of seeds away from adult conspecifics, seed density, fruit pulp removal, and exclusion of introduced mammals.

Finally, in Chapter 6, I conclude by synthesising my findings from each chapter to assess the potential effects of bird declines on seed dispersal in New Zealand, and whether seed dispersal mutualisms are working effectively despite these declines.

Chapter 2: Bird density effects on diet

Bellbird in fruiting *Coprosma robusta*, Hay Reserve, Canterbury. Photo: T. Wyman.

Abstract

Frugivore density can affect competitive interactions between frugivores, both between and among species. Competition can in turn affect foraging behaviour and preferences, and thus diet composition. Optimal foraging theory predicts that diet breadth increases as the total availability of food decreases, so there should be a positive relationship between diet breadth and bird population density. In New Zealand, predation by introduced mammals maintains some mainland and island bird populations below the density at which competition for food and other resources are important influences. Being subject to lower food competition, birds may be more selective, favouring certain 'high-reward' plant species over 'lower-reward' species. I compared fruit removal rates and fruit preferences of birds at sites with high and low bird densities. Five minute bird counts were conducted to obtain an index of relative bird abundance at four sites (Hay, Prices, Lords, and Kaituna) in 2011 and at two sites in 2012 (Hay and Kaituna). These counts showed that both total bird abundance and the abundance of frugivorous bird species were higher at Hay and Prices than Lords and Kaituna. Fruit removal rates of *Melicytus ramiflorus* and *Coprosma* species showed that the proportions of fruit removed at each visit were higher at the high bird sites, and were consistent with preference indices obtained from fruit feeding observations. However, there was a negative relationship between the strength of the site difference in removal rate (measured by the average proportion of fruit removed at high bird site divided by low bird site) and the attractiveness of the plant species (measured by the average proportion of fruit removed across sites). One factor that correlated with how quickly fruits were removed was the total sugars per fruit. The plant species *Coprosma areolata* appeared to be dispersal limited at Kaituna in 2012. The results suggest plants receive better seed dispersal service at high bird sites, and were consistent with the theory that low-reward fruit species suffer most when bird abundance declines. Overall, there was not much evidence for dispersal limitation in Canterbury forest fragments.

Introduction

Frugivore declines can negatively affect plant recruitment through the loss of services provided by these seed dispersing animals, such as facilitating germination, enabling escape from seed predators, increasing gene flow, and enabling colonisation of new sites (Sekercioglu *et al.* 2004). New Zealand has a limited range of vertebrates available to disperse seeds compared to other regions, with no native land mammals (apart from three species of small bat). The native New Zealand terrestrial vertebrate fauna is instead dominated by birds and lizards (Daugherty *et al.* 1993), with birds playing the major role in seed dispersal. Since the relatively recent arrival (ca. 1280 AD) of humans in New Zealand (Wilmshurst *et al.* 2008), nearly half the avifauna and a large proportion of the herpetofauna (lizards) have become extinct (Tennyson 2010), while many extant species have become uncommon or range-restricted, such as kokako (*Callaeas cinerea*), hihi (*Notiomystis cincta*) and saddlebacks (*Philesturnus carunculatus*) (Clout & Hay 1989). Dispersal of fleshy fruits in New Zealand is now largely dependent on four native birds; silvereye (*Zosterops lateralis*), bellbird (*Anthornis melanura*), tui (*Prosthemadera novaeseelandiae*) and kereru (New Zealand pigeon, *Hemiphaga novaeseelandiae*) (Kelly *et al.* 2006).

As well as introducing mammalian predators that caused bird species extinctions and declines, humans also brought with them 38 exotic bird species that established successfully (Tennyson 2010). Three are important seed dispersers in their native countries and are now widespread in New Zealand: blackbird (*Turdus merula*), song thrush (*Turdus philomelos*) and starling (*Sturnus vulgaris*). These exotic birds were considered to be relatively unimportant in the dispersal of native plants in New Zealand (Williams & Karl 1996; Kelly *et al.* 2006), however, more recent studies show that they can make large contributions to native seed dispersal both in terms of quantity of dispersal and the range of plant species they disperse (Chapter 3 of this thesis; Burns 2012; O'Connor 2012). These exotic birds are, however, often less abundant than native birds in native forest systems and the potential for dispersal limitation remains. There have been mainland-island comparisons showing that fruit dispersal is reduced or slowed on the mainland compared to offshore islands where introduced predator numbers are low and native bird numbers are high. For example, Robertson *et al.* (2008) found that there was a higher proportion of ripe and overripe fruit on *Fuchsia excorticata* trees growing on mainland New Zealand compared to those on offshore Kapiti Island, suggesting that fruits are removed more rapidly on the bird sanctuary where bird densities are higher.

Few general ecological patterns have been identified that explain fruit selection by frugivores (Schaefer *et al.* 2003b). Fruit selection is affected by many aspects such as competition with other frugivores, nutrition, fruit morphology and frugivore behaviour (Stoner & Henry 2008). Given the

relative size of frugivores compared to fruits, fruit selection is more likely to be mediated by chemistry than morphology in general (Cipollini & Levey 1997). The exception is for large fruits that depend on large-bodied frugivores for dispersal. There is evidence that frugivores can detect small differences in fruit chemistry (Schaefer *et al.* 2003a). The idea that frugivores will select fruits that best satisfy their nutritional requirements is the basis for the 'nutritional-content hypothesis' (Izhaki 2002). The influence of fruit pulp chemistry on fruit choice in birds is controversial, but some studies have shown that lipid and sugar levels are important (e.g. Fuentes 1994; Herrera 1998). The 'defence trade-off hypothesis' relates fruit removal to the concentration levels of deterrent secondary metabolites and assumes that these compounds represent a trade-off with respect to defence against damaging agents and palatability for dispersers (Cipollini & Levey 1997).

Frugivore density can affect competitive interactions between frugivores, both between and among species. For example, interspecific competition has been observed between tui and bellbirds with tui readily displacing bellbirds from food sites (Craig *et al.* 1981; Ladley & Kelly 1996), while among tui, males typically displace females and older individuals displace younger ones (Stewart & Craig 1985). Competition can in turn affect foraging behaviour and preferences and thus diet composition (Fontaine *et al.* 2008). Optimal foraging theory predicts that diet breadth increases as the total availability of food decreases, e.g. because of competition (Macarthur & Pianka 1966). So there should be a positive relationship between diet breadth and bird population density. In New Zealand, predation by introduced mammals maintains some mainland and island bird populations below the density at which competition for food and other resources are important influences (Innes *et al.* 2010). Being subject to lower food competition, birds may be more selective, favouring certain 'high-reward' plant species over 'lower-reward' species, or avoiding plants that pose greater predation risks such as low-growing shrubs (Anderson *et al.* 2011). Therefore, the decline of avian frugivores has implications for plants that rely on them for seed dispersal and may cause differential selection against certain plant species, resulting in a decline of those species (Anderson 1997). Long-term demographic effects of such dispersal limitation may not be immediately evident due to long life cycles of some plants (Kelly *et al.* 2004), but could have large effects for future populations.

In this study I compare fruit removal rates and fruit preferences of birds at sites with high and low bird densities. I aim to determine the effectiveness of current seed dispersal by investigating fruit removal and relating this to bird abundance. Specific questions I address include: 1) How quickly are fruits removed at high and low bird density sites? 2) Does fruit removal and preference vary with plant species? 3) Is preference related to nutritional content? 4) Are low-reward fruits removed faster by birds at high bird sites than low bird sites?

Methods

Study sites

This study was carried out at four sites in Canterbury, South Island, New Zealand (Fig 2.1). I selected sites to be similar in forest composition; all were lowland podocarp/broadleaved forest remnants, surrounded by farmland.

Lords Bush Scenic Reserve (43°29'S, 171°93'E, 400 m elevation) is a 12 ha remnant of lowland beech/podocarp hardwood forest on the Canterbury Plains. It is located at the base of the Torlesse Range, north of Springfield. *Dacrycarpus dacrydioides* (kahikatea), *Elaeocarpus hookerianus* (pokaka), and *Nothofagus solandri* (black beech) dominate the forest canopy, over a subcanopy of mainly *Griselinia littoralis* (broadleaf) and *Carpodetus serratus* (putaputaweta) (Williams & Buxton 1986). There are also *Prumnopitys taxifolia* (matai), *Coprosma* species, *Pseudowintera colorata* (horopito), *Myrsine divaricata* (weeping matipo), and *Rubus* species present (Williams 2005). Sheep and cattle have grazed in the bush in the past, but it is now partially fenced and a dense scrub of *Ulex europaeus* (gorse) and *Rubus fruticosus* (blackberry) has developed on the margins, limiting ungulate access (Williams & Buxton 1986).

Prices Valley Reserve (43°77'S, 172°71'E, 60 m elevation) is a 4 ha privately owned forest in Banks Peninsula under a QEII National Trust open space covenant (Environment Canterbury 2008). The forest canopy is dominated by *D. dacrydioides*, *Prumnopitys ferruginea* (miro), *P. taxifolia* and *Podocarpus totara* (totara). The undergrowth is dense with abundant podocarp saplings and shrubs such as *Coprosma* species and *Urtica ferox* (nettle), with *Macropiper excelsum* (kawakawa) and *Alectryon excelsus* (titoki) also abundant. (Barker 2009). It is fenced so that stock cannot enter (Environment Canterbury 2008).

Kaituna Valley Scenic Reserve (43°74'S, 172°69'E, 10 m elevation) is a 5.9 ha bush remnant in Banks Peninsula, located 3 km north-west of Prices Valley. The main forest types are *D. dacrydioides*- and *P. taxifolia*-mixed broadleaved forest and *Melicytus ramiflorus* (mahoe) dominated broadleaved forest. *Hoheria angustifolia* (lacebark), *Pennantia corymbosa* (kaikomako), *Streblus heterophyllus* and *Coprosma* species are also present. A notable feature is the dense stand of *A. excelsus*, which is unusual on Banks Peninsula at the southern limit of distribution for this species.

Hay Scenic Reserve (43°70'S, 172°90'E, 35 m elevation) is a 6 ha forest remnant in Pigeon Bay, Banks Peninsula, 18 km north-east of Prices Valley. The forest canopy consists of large *D. dacrydioides*, *P. taxifolia*, *P. ferruginea* and *Podocarpus totara*. There are also *A. excelsus*,

Elaeocarpus dentatus (hinau), *E. hookerianus*, *M. excelsum*, *M. ramiflorus*, *Pittosporum eugenioides* (lemonwood) and *Hedecarya arborea* (pigeonwood). Planted *Populus* and other exotics occur around the edges of the podocarp-hardwood forest, although some of these have been removed in recent years.

At all sites frugivorous birds present include native kereru, silvereye and bellbird, and introduced song thrush, blackbird and starling. Other common birds present are native grey warbler (*Gerygone igata*) and fantail (*Rhipidura fuliginosa*). Tui largely disappeared from Canterbury approximately 20 years ago and are absent at these sites. In 2009 to 2010, 72 tui were reintroduced to Hinewai Reserve, a 1230 ha reserve with intensive mammalian predator control, 18 km south-east of Hay Reserve (Norton & Reid 2013). The birds are successfully fledging young, but were never observed at my study sites.

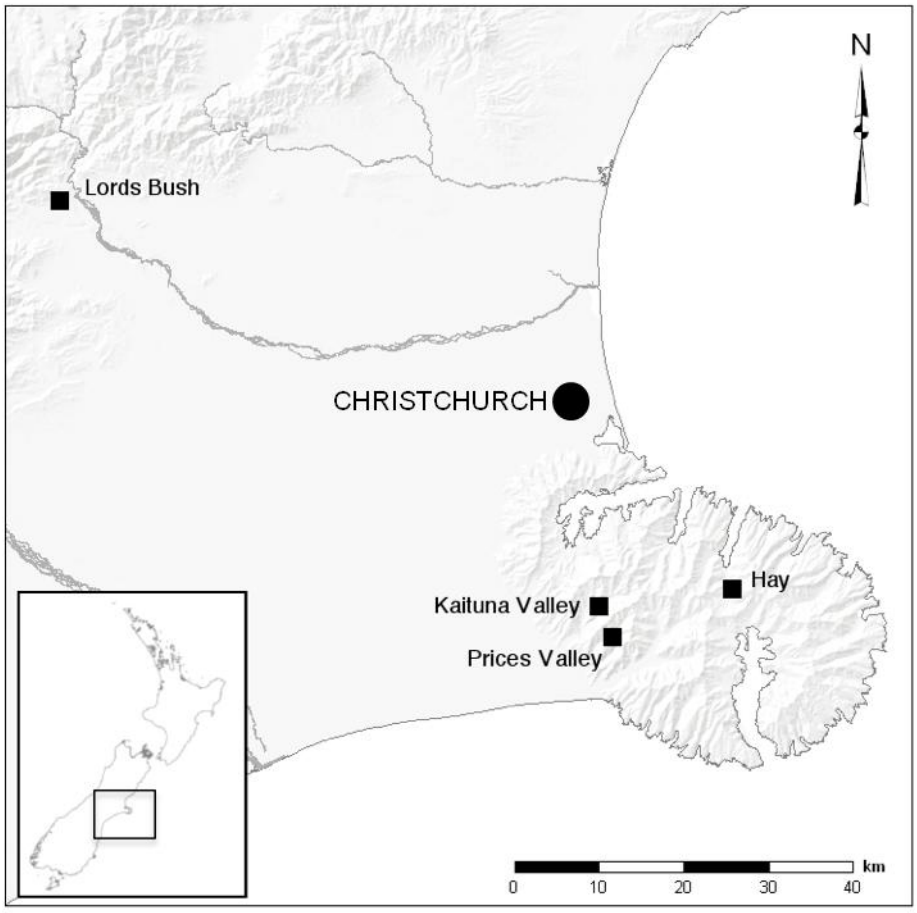

Figure 2.1 Location of study sites relative to Christchurch in the South Island, New Zealand.

Bird counts

To obtain an index of relative bird abundance at the four sites, conventional 5 minute bird counts were carried out. The number and species of birds heard or seen within 100 m during each 5 minute observation session was recorded, following the methods of Dawson and Bull (1975). Bird count stations were 200 m apart and 100 m from the forest edge. Due to the small size of each reserve there were few stations in each; one in each of Kaituna & Hay, two in Prices, and three in Lords. Sites were visited approximately three times per month and counts were repeated 1-3 times per day (morning, noon, evening). To minimize the effects of factors that could influence the detectability of birds, all counts were made by the same observer (myself), counts were made within the period from 1.5 hours after sunrise to 1.5 hours before sunset (to avoid dawn and dusk periods of increased bird conspicuousness), and counts were not conducted during strong winds or heavy rain. Birds flying into or over the count area during the 5 minute period were counted, as long as they were forest bird species (e.g. seabirds were not counted). Within each count, no bird was knowingly counted twice to avoid overestimation of abundance (Dawson & Bull 1975). During 2011, counts were conducted from March to September at all four sites. These counts revealed that Hay and Prices were relatively high-bird sites, and Lords and Kaituna were relatively low-bird sites. During 2012, counts were carried out from March to July at one high-bird site (Hay), and one low-bird site (Kaituna). A total of 18 bird species was recorded over the two years of count data.

Fruit abundance and feeding observations

A preference index was calculated to determine fruit preference using fruit availability and fruit feeding observations. To estimate fruit availability, observations were made during April and May 2011, of the number and ripeness of fruit present along a 200 x 10 m transect line at each site, to determine what fruit was available. All fleshy-fruited fruiting plants present on the transect lines were recorded including species, number of fruits, and percentage of ripe fruit. The number of fruits was estimated visually by dividing the plant into sections, counting the number of fruits on one section of the plant and multiplying by the number of sections on the whole plant. For small shrubs, the total number of fruits on the plant was counted.

Bird-focused feeding observations were carried out along the same transect lines used to measure fruit abundance from March to May 2011. Each transect was traversed in both directions in the morning and afternoon. Transects were walked at a constant pace of 1 km/h and were not walked in adverse weather such as rain or high winds when bird conspicuousness would be reduced. When a bird was encountered, the first foraging event in each 30 second time period was recorded

until visual contact with the bird was lost, up to a maximum of five observations. For every feeding event the following food categories were recorded: (1) fruit (plant species noted); (2) nectar (plant species noted); (3) invertebrate (where the invertebrate could be seen or where the food item could not be seen but where the beak movement and foraging behaviour were consistent with invertebrate foraging); and (4) honeydew.

Fruit preference indices were calculated for bellbirds and silvereyes, as these birds had higher numbers of fruit feeding observations and fed on a range of fruits with which to make comparisons. Jacobs' (1974) food preference index (*D*) was used to calculate fruit preference:

$$D = \frac{r - p}{r + p - 2rp}$$

where *r* is the proportion of a particular fruit species in the diet (proportion of fruit feeding observations), and *p* is the proportional availability of that fruit species in the fruit survey. Jacob's (1974) food preference index gives results from -1 to 1, where positive numbers indicate a food preference and negative numbers indicate an avoidance of a food.

Fruit pulp nutrient analysis

To see whether there was any relationship between fruit nutrient levels and fruit removal by birds, a fruit pulp nutritional analysis was conducted on a number of plant species present at the study sites. Ripe fruits of *Melicytus ramiflorus*, *Coprosma robusta, C. areolata, C. rhamnoides, Dacrycarpus dacrydioides, Ripogonum scandens* and *Elaeocarpus hookerianus* were collected from plants or off the ground, and 50 g of wet fruit flesh from each species was obtained by separating the fruit pulp from the seeds. The fruit pulp samples were delivered to NZ Labs (Auckland) who analysed the nutritional components. The samples were tested on a wet basis and the following components measured; moisture, fat, protein, ash, carbohydrates, energy, sugars (fructose, glucose, lactose, maltose, sucrose and total sugars), and sodium. A sample of 20 fruits of each plant species were weighed before and after removal of seeds to obtain the average wet weight of fruit flesh per fruit.

Fruit removal rates

To compare fruit dispersal service of different plant species at different sites I measured fruit removal rates. I selected *Melicytus ramiflorus* and *Coprosma* species as these plant species had fruits low enough to the ground to be within reach for tagging branches, and had enough fruiting plants to be replicable within a site. Fruit removal rates were monitored for *M. ramiflorus* and *Coprosma*

plants at four sites in 2011. Due to the lack of fruiting plants available, each species could not be measured at all four sites. *Melicytus ramiflorus* fruit removal was measured at Prices, Kaituna and Hay, *C. robusta* at Hay, *C. areolata* at Kaituna, and *C. rhamnoides* at Lords (Table 2.1). These three *Coprosma* species were analysed together as a *Coprosma* genus. In 2012 the method was refined. Hay and Kaituna were selected as these sites had high and low bird densities, respectively (as discovered from the 5 minute bird counts conducted in the previous year), and in that year had sufficient fruiting plants to be able to monitor three species (*M. ramiflorus*, *C. robusta* and *C. areolata*) at each site (Table 2.1).

Fruit removal was measured on 8-10 plants per species per site. On each plant, a branch with 20-100 fruits was tagged so that the fate of the fruit could be followed. As no flowers were present on the branches at the initial visit, no new fruit appeared during the experiments. To confirm that ripe fruit remained on branches in the absence of bird visitors, in 2011 a second branch on each plant with 10-40 fruits was placed inside a muslin bag to exclude animals. Over all plants and sites only one fruit was recovered from the bags, all other ripe and overripe fruit remained attached to the plant, indicating that fruit remains on branches in the absence of bird visitors. The bagging method was not repeated in 2012. The plants were revisited at regular intervals over 3-4 months and the fate of each fruit (unripe, ripe, overripe, or gone from the plant) was recorded. In 2011, the plants were revisited approximately weekly for the first 5 weeks and fortnightly thereafter for the next 2 months. In 2012, the plants were revisited every 3 weeks for 4 months. To determine whether fruits that disappeared from the plants had been dispersed by a bird, or had fallen off the plant, 2 m x 2 m pieces of fabric were laid out underneath each tagged plant to catch any fruits disturbed by birds. The number of whole undispersed fruits caught on the fruit trap underneath each plant was recorded at each visit. Branches were selected for tagging that were not directly adjacent to or below other conspecific fruit that could fall onto the fruit trap. The traps also caught a number of seeds that had been eaten and then voided by birds; these are not presented as it was not known from which plant they came. To check whether any fruits were removed from the fruit traps by animals such as mice, rats or possums (which could cause overestimation of removal rates), I placed five fruits of either *M. ramiflorus*, *C. robusta*, *C. areolata*, or *C. rhamnoides* on two further fruit traps at each site in 2011. The sheets were checked weekly for 3 weeks and all fruits were still present on the fruit traps after the 3 weeks had elapsed, indicating that fruits were not readily removed by ground-dwelling animals.

Table 2.1 Plant species and sites used in fruit removal experiments over two fruiting seasons.

Plant species	2011	2012
Melicytus ramiflorus	Prices, Kaituna, Hay	Kaituna, Hay
Coprosma robusta	Hay	Kaituna, Hay
Coprosma areolata	Kaituna	Kaituna, Hay
Coprosma rhamnoides	Lords	

Data analysis

Bird counts

For analysis of bird counts I selected the six most common frugivorous bird species: bellbird, silvereye, kereru, blackbird, song thrush and starling. All analyses were carried out in the statistical program R, version 2.15.1. Before applying species models, the data were reshaped in R using the reshape package to include all zero counts, giving a new total data set with each species having a data point for each count. A generalized linear model (GLM) with Poisson distribution was used for analysis of bird counts. As I was interested in comparing each year's bird counts to the same year's fruit removal rates, separate models were run for the two years. The nested nature of the data, with a variable number of counts per day (1-3) was accounted for using the sum of counts per day with an offset function in the model. Site and month were included as variables in the model, with subsetting of species. This full model was then simplified using the step function in R to give the model with the lowest AIC score. The example code for analysis of bellbird count data is presented in Appendix 2.1. Since the method used repeat counts through time, a generalised linear mixed model (GLMM) with month as a random effect was also trialled. This model produced very similar results to the GLM, including very similar fitted values, but had some problems running due to the unbalanced nature of the data. The original GLM, being the simpler model, was therefore maintained.

Fruit removal

A GLM was used to test for differences in fruit removal rates between sites, using plants as replicates. The response variable was binomial; based on the proportion of fruits removed of those present at the start of each interval (as opposed to the start of the season; for simplicity, this is referred to as the instantaneous fruit removal rate). Site and Julian day were included as variables in the model. Two separate models were run for *M. ramiflorus* and combined *Coprosma* species in 2011 (since there were not sufficient numbers of fruiting plants to enable site comparisons between

Coprosma species). Data from 2012 allowed separate models to be run for each species (*M. ramiflorus, C. robusta* and *C. areolata*). *A priori* tests showed data were overdispersed; therefore, a quasibinomial error term was specified.

Results

Bird counts

The total number of observations for each bird species in 2011 and 2012 at each site is presented in Table 2.2. A total of 249 counts were made from March to September 2011 (40 at Hay, 66 at Prices, 102 at Lords, and 41 at Kaituna). A total of 92 counts were made from March to July 2012 (49 at Hay and 43 at Kaituna). Overall, 4073 birds were observed, the most common species being bellbirds, followed by silvereyes. Altogether, 18 different species were observed, seven native and ten introduced (Table 2.2). Among the four sites, sulphur-crested cockatoos were unique to Prices, and California quail were only recorded at Kaituna, while a few tomtits, house sparrows and dunnocks were recorded at Lords only. Bellbirds had the highest average counts at all sites except Lords, where silvereyes had higher counts (Table 2.2). A pattern of two high and two low bird sites emerged: Hay and Prices had higher average numbers of birds per count than Lords and Kaituna (Table 2.2). When the average number of birds per count was totalled across the six frugivorous species (bellbird, silvereye, starling, blackbird, kereru, song thrush), Hay and Prices had approximately 11-12 birds per count, while Lords and Kaituna had approximately 5-7 birds per count (Table 2.2).

Seasonally, bellbirds showed the clearest pattern of decrease from March to July/September (Fig 2.2, 2.3). Other birds remained fairly constant throughout the observation period, or did not show clear trends in either direction. Silvereyes appeared to increase at some sites and decrease at others, which may be due to their winter flocking behaviour (Fig 2.2).

The site differences in bird counts were confirmed by the GLMs. Over both seasons there was a significant effect of site on all bird counts except kereru and blackbird counts in 2011 (Table 2.3). In 2011, bellbird and starling counts were higher at Hay and Prices than Lords and Kaituna (Table 2.3a, Fig 2.4). Silvereye counts were higher at Prices and Lords than Hay and Kaituna (Table 2.3a, Fig 2.4). In 2012, counts of bellbird, silvereye, kereru, blackbird and starling were all significantly higher at Hay than Kaituna (Table 2.3b, Fig 2.4). Song thrushes were the only species to have significantly lower counts at Hay than all other sites, and this was observed both years. There were significant effects of month in most cases, however, these changes were similar at all sites as shown by non-

significant site by month interactions. Silvereye counts in 2011 were the only case where monthly changes in counts were different between sites (i.e. significant site × month interaction, Table 2.3a).

Table 2.2 Average number of bird species recorded per 5 minute count at Hay, Prices, Lords and Kaituna. Asterisks indicate introduced bird species. Last row gives the totals for frugivorous birds (bellbird, silvereye, starling, blackbird, kereru and song thrush).

Species	Hay		Prices	Lords	Kaituna	
	2011	2012	2011	2011	2011	2012
Bellbird	5.23	4.84	5.15	2.31	2.05	1.74
Silvereye	2.20	2.20	3.18	3.39	1.88	1.28
Fantail	2.38	1.90	2.11	1.25	1.73	1.14
Starling*	2.15	1.98	1.71	0.29	1.20	1.14
Blackbird*	1.15	1.14	1.12	1.16	0.78	0.67
Grey warbler	0.58	0.65	1.74	0.40	0.88	0.84
Kereru	0.28	0.65	0.32	0.22	0.12	0.21
Song thrush*	0.03	0.06	0.39	0.25	0.20	0.21
Chaffinch*	0.10	0.08	0.05	0.12	0.54	0.53
Cockatoo*	0	0	0.53	0	0	0
Magpie*	0.15	0.18	0.08	0.01	0.15	0.12
California quail*	0	0	0	0	0.27	0.35
Brown creeper	0.25	0.22	0	0	0	0
Greenfinch*	0	0	0	0.03	0.02	0
Tomtit	0	0	0	0.04	0	0
Unknown	0	0	0.02	0.02	0.02	0
House sparrow*	0	0	0	0.03	0	0
Dunnock *	0	0	0	0.01	0	0
Total	14.48	13.92	16.39	9.54	9.83	8.23
Total frugivorous	11.04	10.87	11.87	7.62	6.23	5.25

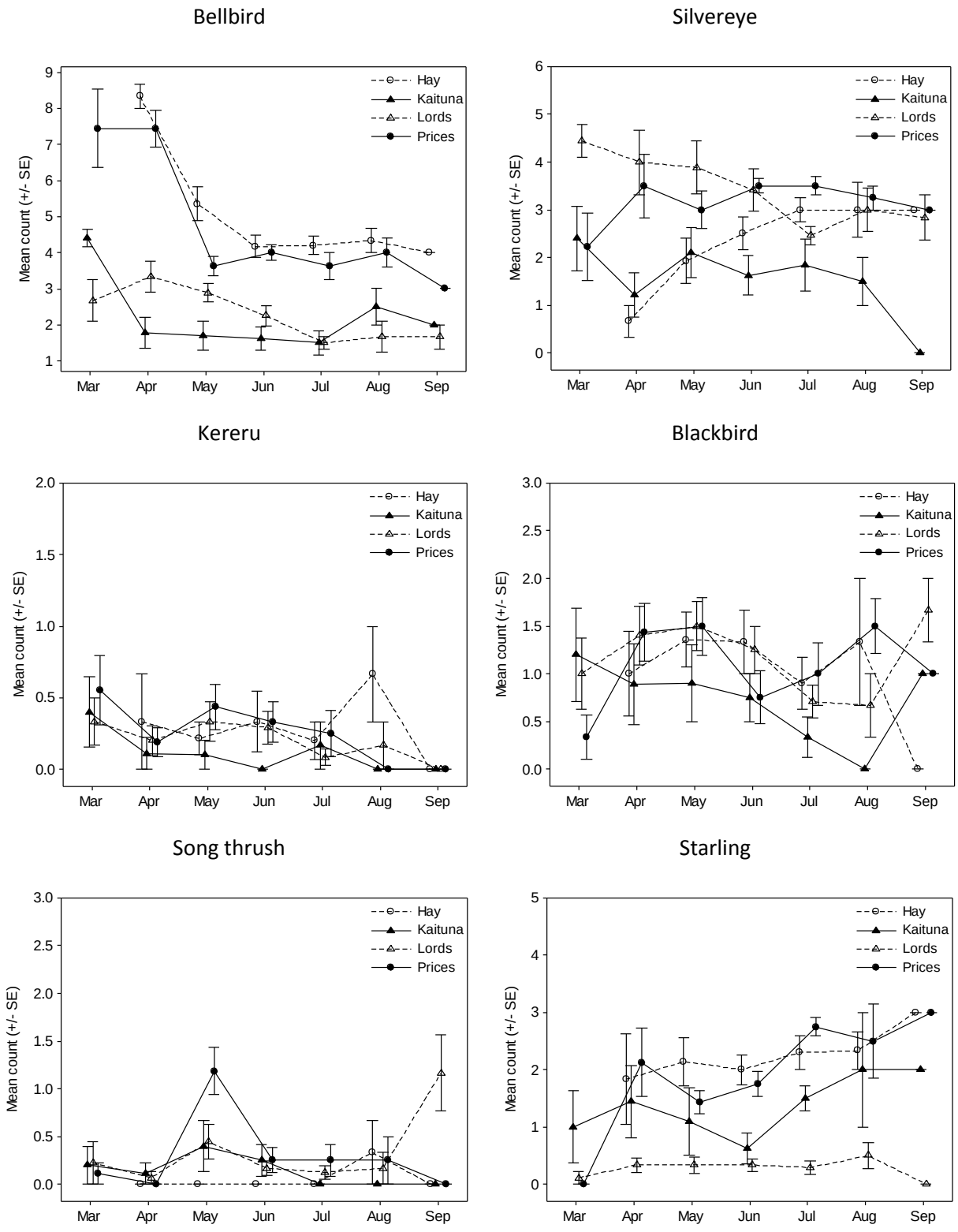

Figure 2.2 Number of birds observed per 5 minute bird count (mean ± SE) at Hay, Kaituna, Lords, and Prices during March to September 2011. Note the varying y-axis scales.

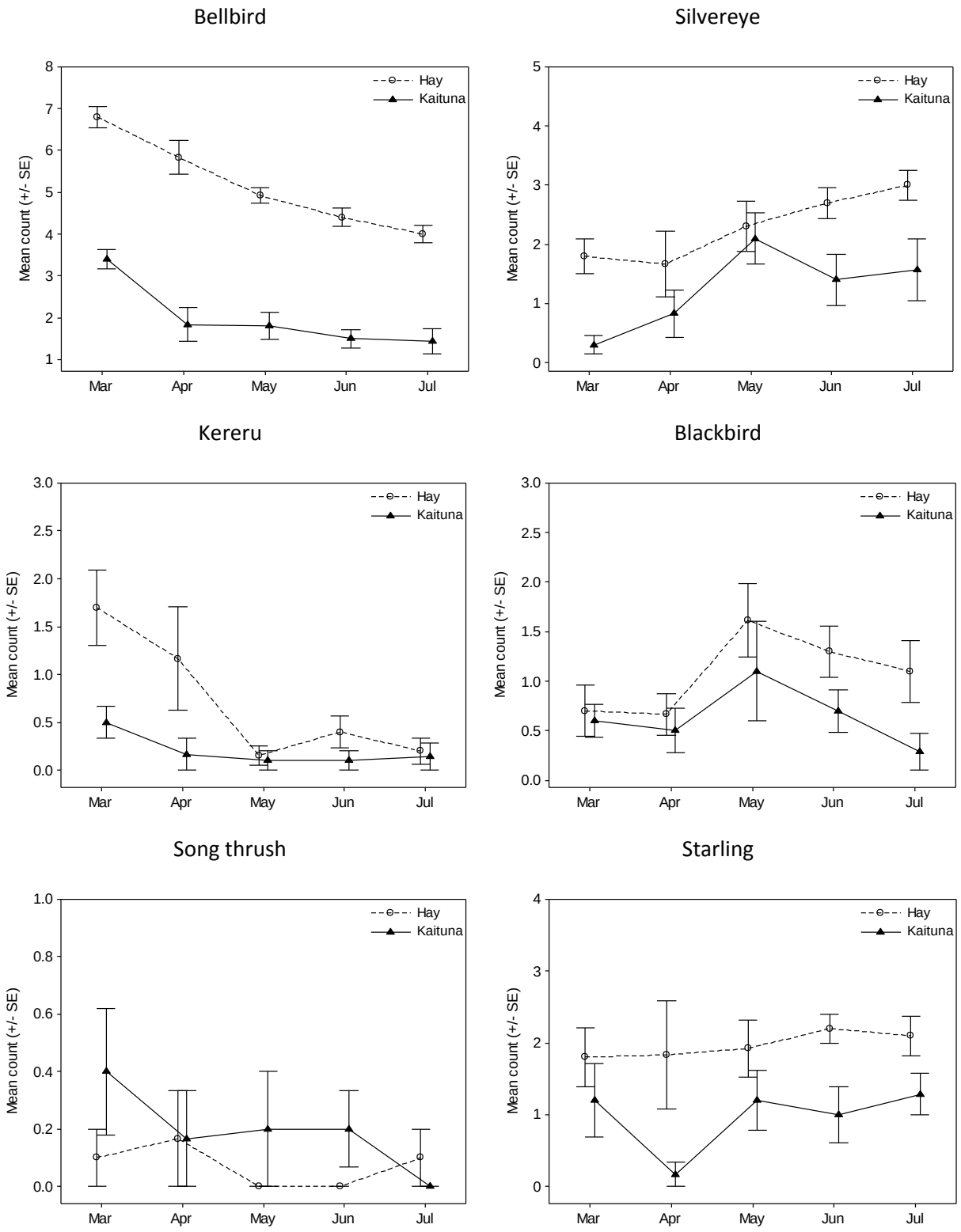

Figure 2.3 Number of birds observed per 5 minute bird count (mean ± SE) at Hay and Kaituna during March to July 2012. Note the varying y-axis scales.

Table 2.3a Poisson generalized linear models with lowest AIC score for 2011 bird counts predicted by site and month.

Species	Predictors	df	Deviance	p value
Bellbird	Site	3	149.991	<0.001
	Month	6	66.124	<0.001
	Residual	113	86.549	
Silvereye	Site	3	39.720	<0.001
	Month	6	2.431	0.876
	Site:Month	17	35.181	0.006
	Residual	96	139.880	
Kereru	Residual	122	113.490	
Blackbird	Month	6	13.600	0.034
	Residual	116	125.200	
Song thrush	Site	3	18.560	<0.001
	Month	6	43.520	<0.001
	Residual	113	107.630	
Starling	Site	3	135.976	<0.001
	Month	6	26.786	<0.001
	Residual	113	166.48	

Table 2.3b Poisson generalized linear models with lowest AIC score for 2012 bird counts predicted by site and month.

Species	Predictors	df	Deviance	p value
Bellbird	Site	1	61.868	<0.001
	Month	4	18.256	0.001
	Residual	33	8.739	
Silvereye	Site	1	15.275	<0.001
	Month	4	13.905	0.008
	Residual	33	27.957	
Kereru	Site	1	10.853	<0.001
	Month	4	29.340	<0.001
	Residual	33	39.175	
Blackbird	Site	1	5.562	0.018
	Month	4	8.436	0.077
	Residual	33	28.172	
Song thrush	Site	1	3.974	0.046
	Residual	37	29.766	
Starling	Site	1	14.098	<0.001
	Residual	37	82.210	

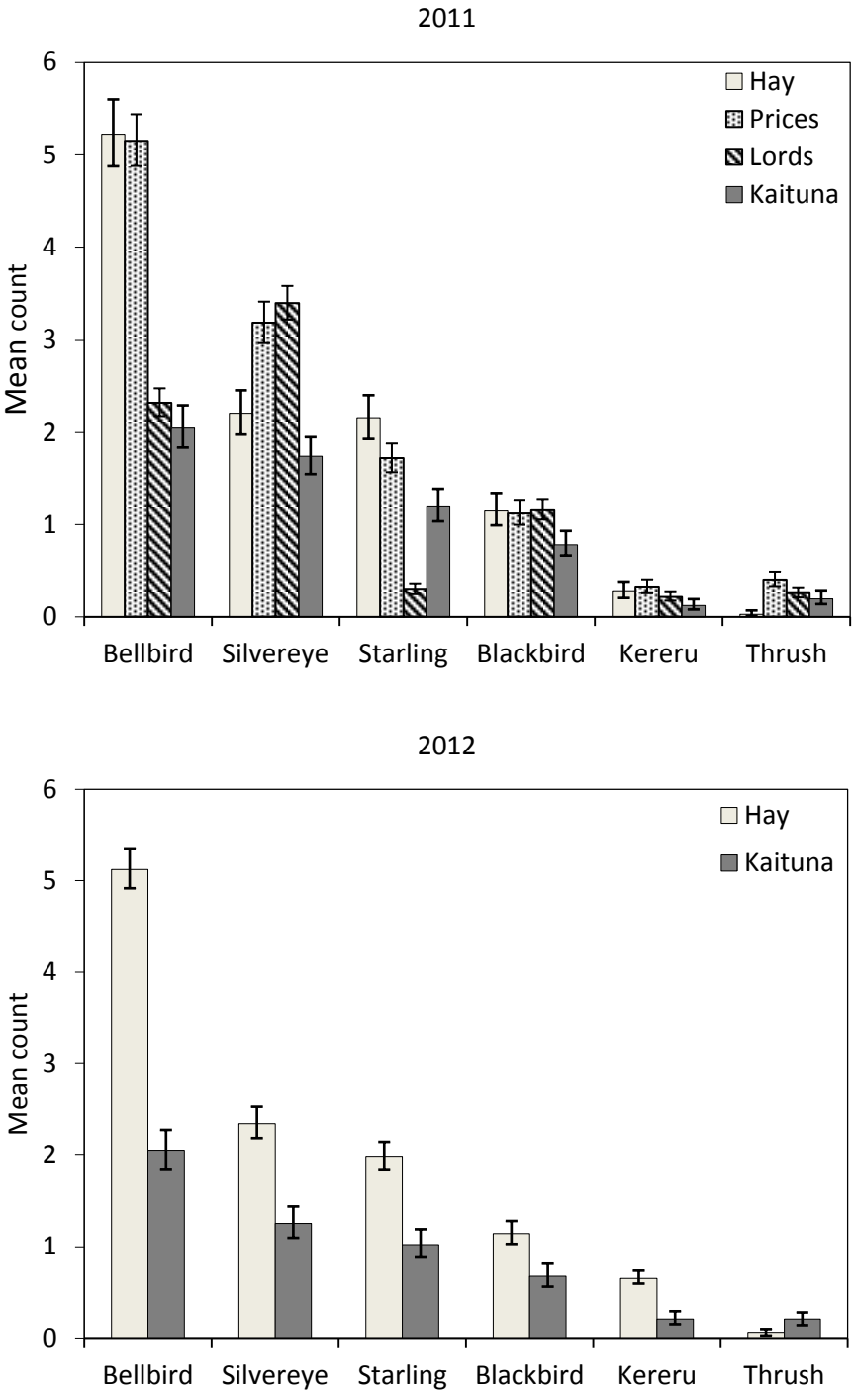

Figure 2.4 Number of frugivorous birds recorded per 5 minute count in 2011 and 2012 (mean ± SE). Values are back-transformed fitted means from a Poisson GLM, with site as the only factor.

Fruit abundance and feeding observations

A total of 370 feeding observations were made during March to June 2011. Of these feeding observations, 78% were of fruit, 16% invertebrates, and 5% honeydew (Table 2.4). Bellbirds and silvereyes fed on all three of these food types, with fruit making up the highest proportion of the diet. Kereru and starlings were only observed feeding on fruit, although there were few observations of starlings. Kereru and starlings fed almost entirely in the upper canopy, which made sightings more difficult, especially for starlings. There were few observations of blackbirds and song thrushes, and no fruit feeding observations, although they are known to include a large proportion of fruit in their diet (see Chapter 3). These birds were usually disturbed and flew away before an observation could be made.

Table 2.4 Food types of forest birds in Hay, Prices, Lords and Kaituna (percent of observed diet). n = number of feeding observations.

Bird species	n	Fruit	Honeydew	Invertebrate
Bellbird	160	75.6	11.9	12.5
Silvereye	129	91.5	0.8	7.8
Kereru	43	100	0	0
Blackbird	3	0	0	100
Song thrush	6	0	0	100
Starling	6	100	0	0
Fantail	7	28.6	0	71.4
Grey warbler	16	0	0	100

Hay had the highest number of fruits per hectare, approximately four times as many as Kaituna (Table 2.5). Hay also had the largest number of fruiting plant species present, twice as many as Kaituna. *Dacrycarpus dacrydioides* fruit was present at all sites and in the highest quantity overall. *Melicytus ramiflorus* was the second most common fruit, present at all sites except Lords. Fruit feeding was observed on 16 plant species over all four sites, with most observations on *M. ramiflorus* (Table 2.5). Bellbirds and silvereyes fed on a range of fruit species, with most observations again on *M. ramiflorus.* Over all sites, silvereyes ate 11 different fruit species, and bellbirds nine (Table 2.5). Starlings were only observed feeding on fruit of a single species, *D. dacrydioides*, at one site. Kereru were observed feeding solely on *D. dacrydioides* fruit at three sites (Hay, Prices and Kaituna), and at the other (Lords) they fed solely on *Elaeocarpus hookerianus* fruit, even though *D. dacrydioides* fruit was also available. *Elaeocarpus hookerianus* was available at Lords Bush only.

Table 2.5 Fruit abundance (per hectare), percentage of fruits in the forest and percentage of fruits in feeding observations for birds that fed on fruit in 2011 at Hay, Prices, Lords and Kaituna.

Site	Plant species	Fruit/ha	Percentage of fruit	Percentage of feeding observations			
				Bellbird	Silvereye	Kereru	Starling
Hay	*Dacrycarpus dacrydioides*	255000	53.70	0	0	100	100
	Melicytus ramiflorus	4575	0.96	17.5	17.4	0	0
	Pseudopanax arboreus	134650	28.36	0	8.7	0	0
	Myrsine australis	59000	12.42	0	43.5	0	0
	Pittosporum eugenioides	11000	2.32	1.8	30.4	0	0
	Coprosma robusta	4000	0.84	35.1	0	0	0
	Coprosma areolata	1000	0.21	0	0	0	0
	Ripogonum scandens	3810	0.80	3.5	0	0	0
	Macropiper excelsum	1030	0.22	42.1	0	0	0
	Passiflora tetrandra	600	0.13	0	0	0	0
	Alectryon excelsus	200	0.04	0	0	0	0
	Total	474865	100	100	100	100	100
Prices	*Dacrycarpus dacrydioides*	100000	44.96	7.3	0	100	0
	Melicytus ramiflorus	92825	41.73	48.8	52.5	0	0
	Melicytus micranthus	19700	8.86	39.0	10.0	0	0
	Pittosporum eugenioides	2500	1.12	0	0	0	0
	Lophomyrtus obcordata	4400	1.98	0	12.5	0	0
	Pittosporum tenuifolium	3000	1.35	4.9	25.0	0	0
	Total	222425	100	100	100	100	0
Lords	*Dacrycarpus dacrydioides*	100000	32.05	0	38.9	0	0
	Elaeocarpus hookerianus	155000	49.67	0	0	100	0
	Coprosma rhamnoides	52670	16.88	0	0	0	0
	Neomyrtus pedunculata	4025	1.29	100	22.2	0	0
	Carpodetus serratus	250	0.08	0	38.9	0	0
	Pseudowintera colorata	100	0.03	0	0	0	0
	Total	312045	100	100	100	100	0
Kaituna	*Dacrycarpus dacrydioides*	50000	44.09	0	0	100	0
	Melicytus ramiflorus	56603	49.91	72.2	80.0	0	0
	Coprosma robusta	3000	2.65	27.8	0	0	0
	Coprosma areolata	2995	2.64	0	0	0	0
	Pennantia corymbosa	813	0.72	0	20.0	0	0
	Total	113411	100	100	100	100	0

Fruit preference indices were calculated for bellbirds and silvereyes as these birds had higher numbers of fruit feeding observations and fed on a range of fruits with which to make comparisons (Table 2.6). *Melicytus ramiflorus* fruit was consistently favoured by bellbirds and silvereyes where it was available. *Coprosma robusta* fruit was favoured by bellbirds (consistent with results from Chapter 3), but silvereyes were not observed eating it.

Table 2.6 Preference of bellbirds and silvereyes for fruit species at Hay, Prices, Lords and Kaituna in 2011 (Jacob's food preference index: +1, strongly selected; -1, strongly avoided), highlighted numbers are positive, indicating a preference.

Site	Plant species	Bellbird	Silvereye
Hay	*Dacrycarpus dacrydioides*	-1	-1
	Melicytus ramiflorus	0.91	0.91
	Pseudopanax arboreus	-1	-0.61
	Myrsine australis	-1	0.69
	Pittosporum eugenioides	-0.14	0.90
	Coprosma robusta	0.97	-1
	Coprosma areolata	-1	-1
	Ripogonum scandens	0.64	-1
	Macropiper excelsum	0.99	-1
	Passiflora tetrandra	-1	-1
	Alectryon excelsus	-1	-1
Prices	*Dacrycarpus dacrydioides*	-0.82	-1
	Melicytus ramiflorus	0.14	0.21
	Melicytus micranthus	0.74	0.07
	Pittosporum eugenioides	-1	-1
	Lophomyrtus obcordata	-1	0.75
	Pittosporum tenuifolium	0.58	0.92
Lords	*Dacrycarpus dacrydioides*	-1	0.15
	Elaeocarpus hookerianus	-1	-1
	Coprosma rhamnoides	-1	-1
	Neomyrtus pedunculata	1.00	0.91
	Carpodetus serratus	-1	1.00
	Pseudowintera colorata	-1	-1
Kaituna	*Dacrycarpus dacrydioides*	-1	-1
	Melicytus ramiflorus	0.45	0.60
	Coprosma robusta	0.87	-1
	Coprosma areolata	-1	-1
	Pennantia corymbosa	-1	0.94

Fruit pulp nutrient analysis

Melicytus ramiflorus fruit pulp had the highest percent total sugars and protein of all the species analysed. It also had the second highest (to *Elaeocarpus hookerianus*) percent carbohydrate and energy (Table 2.7). *Elaeocarpus hookerianus* fruit is quite different to the other species in that it has dry, fibrous pulp, reflected in the low percent moisture compared to the other species. It also had a very high percent carbohydrate and energy, and a very low percent total sugars. *Coprosma areolata* had the highest percent fat, and by far the highest percent sodium.

Table 2.7 Nutritional contents of the fruit pulp of seven plant species used in this study. Values are based on the wet weight of fruit pulp.

Nutrient	Unit	*Mel ram*	*Cop rob*	*Cop are*	*Cop rha*	*Dac dac*	*Rip sca*	*Ela hoo*
moisture	%m/m	77.60	86.70	78.70	90.9	83.8	86.9	50.8
fat	g/100g	0.45	1.23	1.26	0.63	0.84	0.20	0.39
protein	g/100g	1.58	0.47	1.16	0.43	1.45	0.60	1.37
ash	%m/m	1.02	0.77	1.84	0.64	0.96	1.31	0.73
total sugars	%m/m	12.60	6.86	1.63	4.59	4.52	2.65	0.07
fructose	%m/m	6.01	4.26	1.00	1.41	2.80	1.36	<0.02
glucose	%m/m	6.55	2.60	0.63	3.16	1.72	1.29	0.07
carbohydrate	g/100g	19.40	10.80	17.10	7.4	13	11	46.7
energy	kJ/100g	373	237	356	156	277	204	832
sodium	mg/100g	7.25	3.95	58	8.16	7.07	3.57	<2.00
pulp weight per fruit	mg	48	69	39	41	125	501	450

Collection date and source sites for samples: *Melicytus ramiflorus*, 22/5/11, Kaituna Valley; *Coprosma robusta*, 3/5/11, Blue Duck Reserve, Kaikoura; *Coprosma areolata*, 5/6/12, Kaituna Valley; *Coprosma rhamnoides*, 20/5/11, Lords bush; *Dacrycarpus dacrydioides*, 13/5/11, Riccarton Bush, Christchurch; *Ripogonum scandens*, 5/5/11, Lake Waikaremoana, Hawkes Bay; *Elaeocarpus hookerianus*, 20/5/11, Lords Bush.

Fruit removal rates

At the beginning of the 2011 fruit removal monitoring, the percentage of fruit removed per day (of the initial number of fruit at the start of the season) for both *M. ramiflorus* and *Coprosma* species was higher at Prices and Hay than at Lords and Kaituna (Fig 2.5). As the season progressed and the number of fruits available for removal decreased, absolute rates of fruit removal slowed and the sites became more similar. After approximately three months, the percentage of fruits removed per day was close to zero as most fruits had already been removed.

A similar pattern was observed in 2012 for *M. ramiflorus* and *C. robusta.* These two species were removed at higher rates at Hay than at Kaituna at the start of the monitoring period, but then as the season progressed and the number of fruits remaining decreased, the rates became more similar (Fig 2.6). Removal of *C. areolata*, however, showed a different pattern; removal remained consistently low throughout the season at both sites, although higher at Hay (mean 0.74% removed per day) than Kaituna (mean 0.48% removed per day) (Fig 2.6). Nearly all *M. ramiflorus* and *C. robusta* fruits had been removed by the final 2012 count at both sites (means between 99 - 100%), compared with 92% of *C. areolata* fruits at Hay, and 59% of *C. areolata* fruits at Kaituna. Fruits still remaining at the final count were typically overripe, dry and shrivelled.

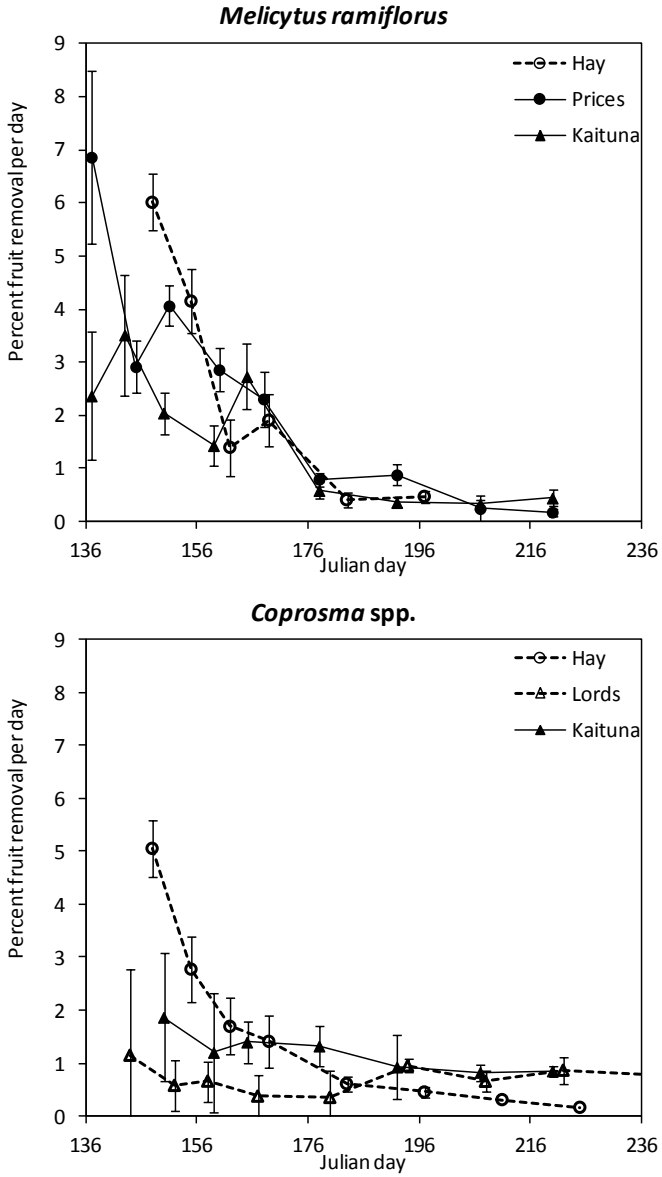

Figure 2.5 Percent fruit removal per day (mean percent of the initial number of fruit at the start of the season ± SE) for *Melicytus ramiflorus* at Hay, Prices and Kaituna, and *Coprosma* species at Hay, Lords and Kaituna in 2011.

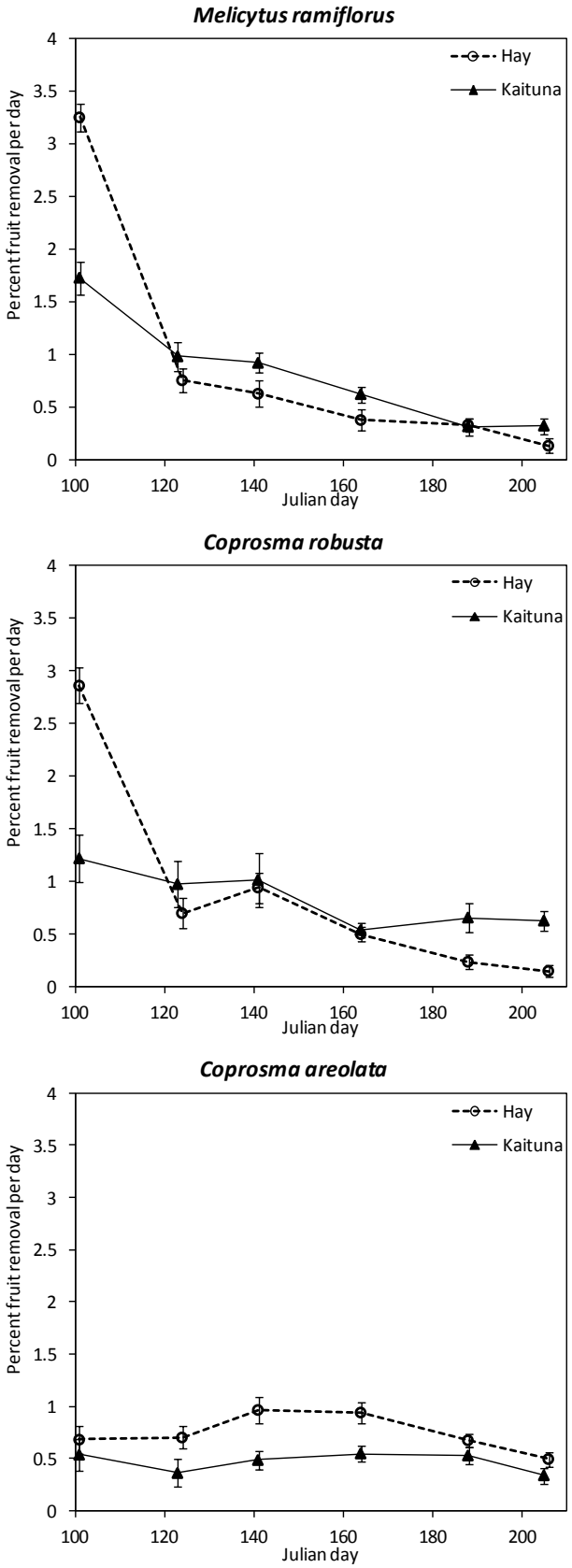

Figure 2.6 Percent fruit removal per day (mean percent of the initial number of fruit at the start of the season ± SE) for *Melicytus ramiflorus*, *Coprosma robusta* and *Coprosma areolata* at Hay and Kaituna in 2012.

The GLMs based on the proportion of fruit removed in each interval (the instantaneous fruit removal rate), confirmed the site differences (Table 2.8, 2.9). In 2011, the proportion of *M. ramiflorus* fruit removed in each interval was significantly higher at Hay than Kaituna and Prices (Table 2.8b, Fig 2.7). There was a significant effect of day, meaning that the proportion of fruit removed changed over the season, and these changes were similar at all sites, indicated by non-significant site by day interactions. Removal of *Coprosma* fruit was higher at Hay than Kaituna and Lords, and there was a significant effect of day and a significant site by day interaction (Table 2.8b, Fig 2.7).

In 2012, removal of *M. ramiflorus*, *C. robusta* and *C. areolata* was significantly higher at Hay than Kaituna (Table 2.9, Fig 2.7). There was a significant effect of day on removal for all species, and a significant site by day interaction for *M. ramiflorus* and *C. areolata.*

Table 2.8a Quasibinomial generalized linear models for 2011 instantaneous fruit removal predicted by site and Julian day.

Species	Predictors	df	Deviance	p value
Melicytus ramiflorus	Site	2	128.67	<0.001
	Day	1	56.96	<0.001
	Residual	164	593.63	
Coprosma spp.	Site	2	338.31	<0.001
	Day	1	628.74	<0.001
	Site:Day	2	65.23	<0.001
	Residual	217	453.80	

Table 2.8b Model coefficients for quasibinomial generalized linear models for 2011 instantaneous fruit removal.

Species	Predictors	Estimate	Std. error	t value	p value
Melicytus ramiflorus	Intercept	-2.459	0.580	-4.241	<0.001
	SiteKaituna	-1.178	0.198	-5.961	<0.001
	SitePrices	-0.548	0.214	-2.563	0.011
	Day	0.015	0.004	4.157	<0.001
Coprosma spp.	Intercept	-1.017	0.186	-5.463	<0.001
	SiteKaituna	-1.886	0.457	-4.123	<0.001
	SiteLords	-3.284	0.266	-12.337	<0.001
	Day	0.008	0.004	1.997	0.047
	SiteKaituna:Day	0.021	0.008	2.559	0.011
	SiteLords:Day	0.025	0.005	5.440	<0.001

Table 2.9a Quasibinomial generalized linear models for 2012 instantaneous fruit removal predicted by site and Julian day.

Species	Predictors	df	Deviance	p value
Melicytus ramiflorus	Site	1	41.22	<0.001
	Day	1	26.76	0.004
	Site:Day	1	16.88	0.020
	Residual	100	338.28	
Coprosma robusta	Site	1	58.10	<0.001
	Day	1	70.93	<0.001
	Residual	103	369.24	
Coprosma areolata	Site	1	34.81	<0.001
	Day	1	125.68	<0.001
	Site:Day	1	17.26	0.001
	Residual	116	200.67	

Table 2.9b Model coefficients for quasibinomial generalized linear models for 2012 instantaneous fruit removal.

Species	Predictors	Estimate	Std. error	t value	p value
Melicytus ramiflorus	Intercept	0.123	0.497	0.248	0.804
	SiteKaituna	-2.021	0.640	-3.157	0.002
	Day	-0.000	0.004	-0.106	0.916
	SiteKaituna:Day	0.012	0.005	2.368	0.020
Coprosma robusta	Intercept	-1.708	0.367	-4.652	<0.001
	SiteKaituna	-0.848	0.163	-5.179	<0.001
	Day	0.014	0.003	4.714	<0.001
Coprosma areolata	Intercept	-4.734	0.473	-10.006	<0.001
	SiteKaituna	1.38	0.674	2.052	0.042
	Day	0.027	0.003	8.240	<0.001
	SiteKaituna:Day	-0.015	0.005	-3.265	0.001

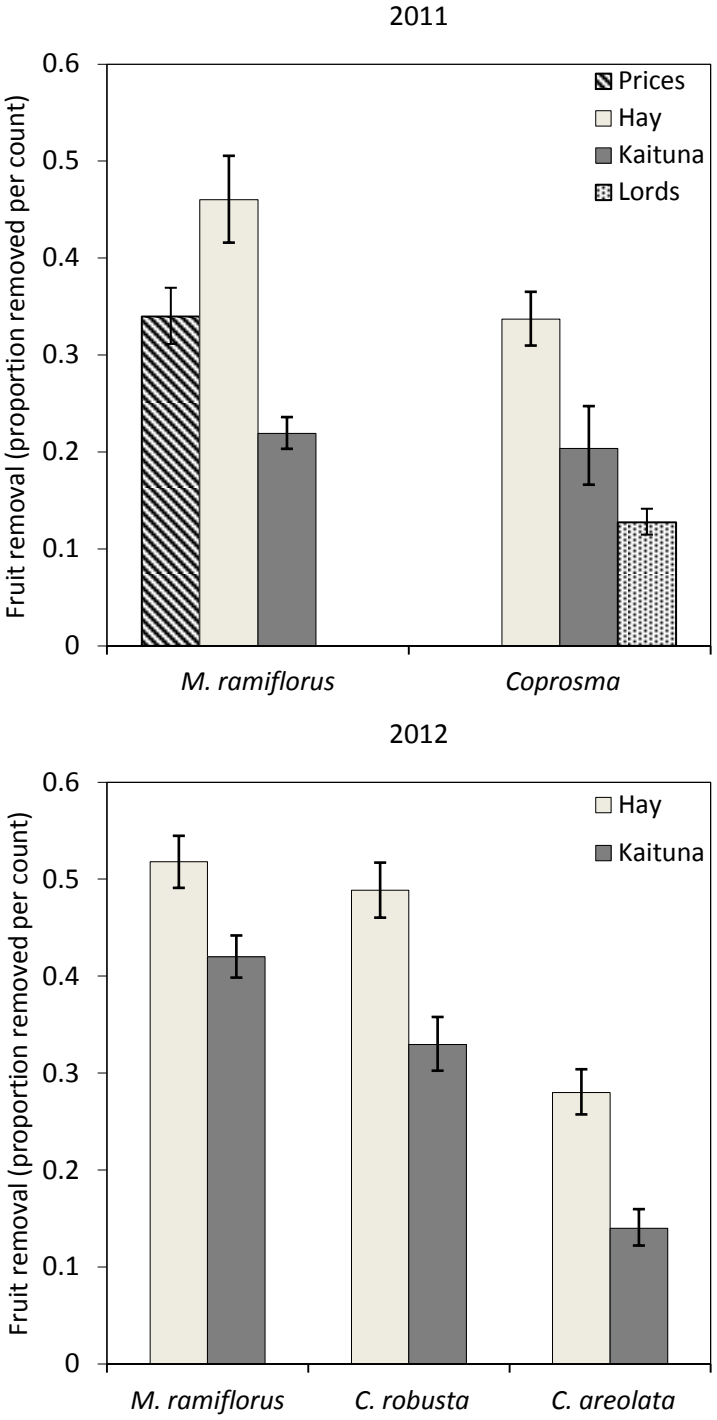

Figure 2.7 The average proportion of fruit removed per count (± SE). Values are back-transformed fitted means from a quasibinomial GLM, with site as the only factor.

Using the 2012 fruit removal data I looked at the relationship between the strength of the site difference in removal rate (measured by the average proportion of fruit removed at Hay divided by Kaituna) and the attractiveness of the plant species (measured by the average proportion of fruit removed across sites). Across the three plant species there was an apparent negative relationship

between the strength of the site difference in removal rate and the attractiveness of the plant (Fig 2.8). The difference in removal rate between Hay and Kaituna was highest for *C. areolata* (removal rate at Hay approximately double that of Kaituna), and this species was the least attractive. In contrast, *M. ramiflorus* was removed more equally at both sites (removal rate at Hay/Kaituna = 1.2), and was the most attractive.

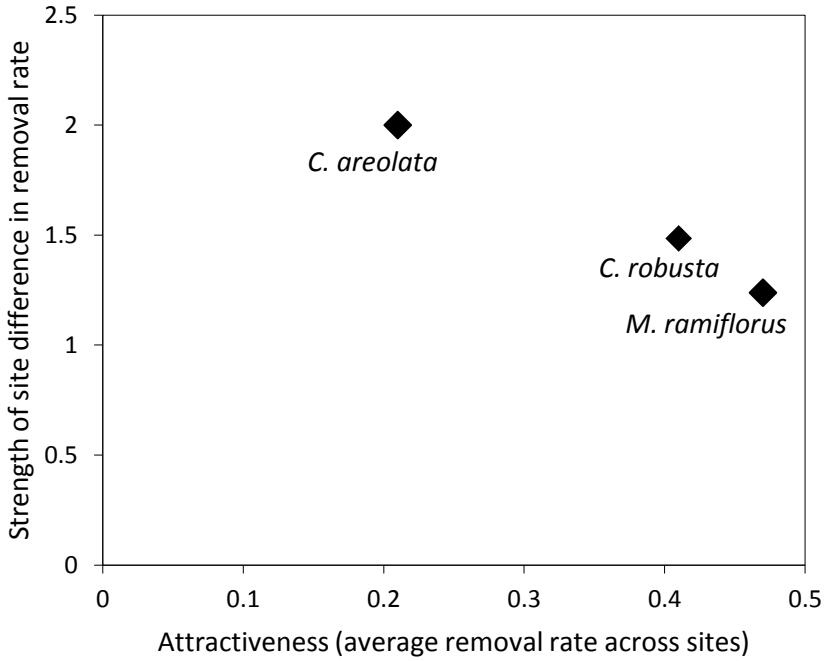

Figure 2.8 Strength of site difference in average removal rate (measured by the average proportion of fruit removed at Hay divided by that at Kaituna) as a function of the attractiveness (measured by the average proportion of fruit removed across sites) for the three plant species; *Coprosma areolata*, *Coprosma robusta* and *Melicytus ramiflorus* in 2012.

There was a negative correlation between fruit persistence (the number of days until half the number of fruits were removed, calculated by interpolating between data points) and the total sugars per fruit (percent total sugars obtained from nutrient analysis multiplied by the pulp weight per fruit). *Melicytus ramiflorus* was removed fastest at both Hay and Kaituna, and had the highest total sugars per fruit, followed by *C. robusta*, and *C. areolata* with the lowest (Fig 2.9). There were too few data for a formal correlation test (n=3), but the results are consistent with longer persistence times of lower-reward fruits, and shorter persistence times at high bird sites.

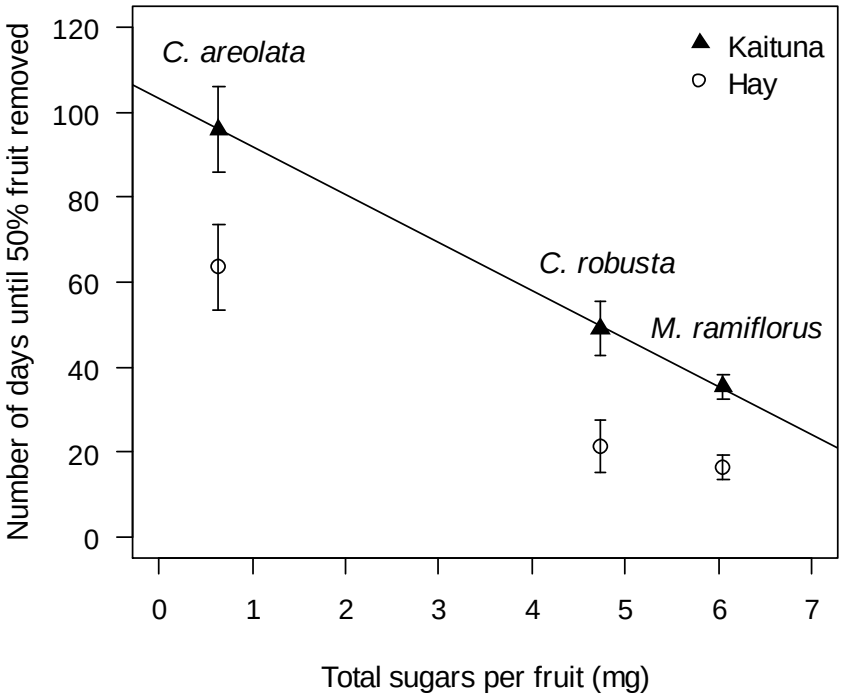

Figure 2.9 Relationship between the number of days until half the number of fruits on tagged branches were removed (± SE) and the total sugars per fruit for *Melicytus ramiflorus*, *Coprosma robusta* and *Coprosma areolata* at a high (Hay) and low (Kaituna) bird site in 2012.

Discussion

The results of this study suggest that plant species receive better dispersal service at Hay and Prices than at Kaituna and Lords. At Hay and Prices, key fruit dispersing birds were more abundant and fruits were removed more quickly. The increased dispersal service was not equal among plant species however, with the attractiveness of the plant determining how much faster fruits were removed at high bird sites.

Bird counts

Overall, Hay and Prices had higher bird abundances than Kaituna and Lords. Bellbirds, in particular, were present at much higher levels at the high bird sites and are important frugivores. The next most common frugivorous species in the bird counts were silvereyes and starlings (although there were few sightings of starlings actually feeding on fruit). The difference between sites for these birds was less than for bellbirds, but Hay still had significantly higher counts than Kaituna. It should be noted that 5 minute bird counts provide only an index of abundance, rather than a measure of

absolute density (Murphy & Kelly 2001; Innes *et al.* 2003). The sites used for this study were selected to be similar in forest composition; all were lowland podocarp/broadleaved forest remnants of similar size. However, the fruit abundance surveys revealed site differences in the number of fruits per hectare and also the number of fruiting plant species. Kaituna had the lowest fruit abundance and number of fruiting species recorded in the fruit surveys. This could be one factor contributing to the lower bird abundances recorded there. Estimates of bird density using 5 minute counts have suggested that native birds occur in higher numbers in habitats of more diverse vegetation (Clout & Gaze 1984). Bellbird counts (in particular) decreased through the monitoring period with the highest counts in March through to the lowest counts in winter/spring in both years and at most sites. Murphy and Kelly (2001) found that bellbird counts in Craigieburn also peaked in March before decreasing through the winter. This seasonal variation is consistent with either a change in bellbird numbers, or seasonal variation in bellbird conspicuousness, or both. However, Gibb (1996) stated that bellbirds in the Orongorongo Valley, Wellington, have a high frequency of calling and singing throughout the year with little seasonal variation in conspicuousness. This suggests that the seasonal variation is due to a change in bellbird numbers, presumably due to movement of birds into other forest patches nearby, rather than a change in conspicuousness.

Feeding observations

By far, most feeding observations recorded were for bellbirds and silvereyes, and these birds included a large proportion of fruit in their diet. Kereru and starlings were only observed feeding on fruit, although there were few observations of starlings. Starling observations were particularly difficult as they fed almost entirely in the upper canopy. Although included as frugivores in the analysis, blackbirds and song thrushes were never actually observed feeding on fruit. Blackbirds and song thrushes are known to include a large proportion of fruit in their diet (Chapter 3 of this thesis; Burns 2012; O'Connor 2012), however, it has been suggested that they are relatively unimportant dispersers of native fruits (Williams & Karl 1996; Kelly *et al.* 2006). These birds were easily disturbed and flew away before feeding observations could be made. Feeding observations appear to be a relatively ineffective method for quantifying seed dispersal by blackbirds and song thrushes in particular, due to their wariness of people. Chapter 3 will use a different method to explore further the importance of these species as frugivores.

Starlings were only observed feeding on *Dacrycarpus dacrydioides* fruit, and kereru fed only on *D. dacrydioides* and *Elaeocarpus hookerianus* fruit. *Dacrycarpus dacrydioides* produces high quantities of fruit, high up in the canopy, which may be why this plant species was preferred by starlings and

kereru, whereas bellbirds and silvereyes preferred to feed in the understory (consistent with O'Donnell & Dilks 1994). Kereru preferred *Elaeocarpus hookerianus,* which is a large, dry, carbohydrate-rich and sugar-poor fruit that provides a lot of energy. To my knowledge, only one study has reported kereru feeding on *E. hookerianus,* and observations occurred only once or twice (McEwen 1978), though kereru are known to feed on *Elaeocarpus dentatus* (Clout & Hay 1989; Emeny *et al.* 2009), which has a very similar fruit (Dijkgraaf 2002).

Fruit removal rates

Fruit removal was higher for *M. ramiflorus* and *C. robusta* than *C. areolata* in 2012. This was consistent with results from the fruit feeding observations. Fruit preferences varied across sites, but bellbirds and silvereyes had mild to strong preferences for *M. ramiflorus* where it was available, and bellbirds favoured *C. robusta* (consistent with Chapter 3). No birds were observed taking *C. areolata* fruit. Fruit selection by birds is a complex process, with the literature suggesting that nutritional qualities, morphology, spatial arrangement of fruit, and fruit crop size are all important factors (Izhaki 2002). In terms of nutritional quality, sugars and lipids have been found to be important components for fruit preference (Fuentes 1994; Herrera 1998; Schaefer *et al.* 2003b). Basic fruit morphological characteristics such as size or colour did not appear to affect removal in this case. Fruits of *M. ramiflorus* and the *Coprosma* species used in this study were of a broadly similar size (approximately 3-5 mm diameter), and coloured either red (*C. robusta, C. rhamnoides*) or dark purple (*M. ramiflorus*, *C. areolata*). One factor that was correlated with how quickly fruits were removed in this study was the total sugars per fruit. However, there could be multiple explanations for the differences in fruit removal rates, either working in conjunction with the level of sugars (such as lower levels of secondary compounds), or birds may be basing their choice on something completely different, such as selecting for a particular mineral (e.g. calcium; O'Brien *et al.* 1998).

Effect of bird declines on fruit removal

Low bird densities in New Zealand forests have previously been suggested as possible limiting factors for fruiting plant species (Ladley & Kelly 1996; Anderson 1997; McNutt 1998). Mainland-island comparisons suggest that the fruit dispersal of *Fuchsia excorticata*, *Rhopalostylis sapida*, and *Pittosporum crassifolium* is reduced or slowed by a lack of frugivores on the mainland (McNutt 1998; Anderson *et al.* 2006; Robertson *et al.* 2008). Similar effects of low bird densities have also been found overseas. For example, in Spain, Herrera *et al.* (1994) compared fruit removal of *Phillyrea latifolia* at two sites with different abundances of seed dispersing birds and found that birds

removed 78% of the fruit crop at the site with more seed dispersers, and 33% at the site with fewer dispersers.

The difference in fruit removal rates between Hay and Kaituna was smaller for *C. robusta* and *M. ramiflorus* than for *C. areolata*, where the relative removal rate at Hay was double that at Kaituna. This difference could be due to the higher bird densities at Hay, leading to increased food competition for the more favoured fruits so that birds are forced to include more of the less attractive fruit in their diet (Redford & Feinsinger 2001). In contrast, at Kaituna, which has lower bird densities, there may be less competition for food so birds can be more selective and only take the higher-reward fruits. Although there was a lower overall fruit abundance at Kaituna than Hay, the abundance of *M. ramiflorus* fruit was higher at Kaituna (56600 compared with 4500 fruit per hectare), and the abundance of *C. robusta* was similar (3000 compared with 4000 fruit per hectare). Higher or similar fruit abundance of *M. ramiflorus* and *C. robusta* at Kaituna, combined with lower bird densities would support the idea that competition for these fruit species is lower at Kaituna than at Hay. In the context of New Zealand's bird declines, these sorts of interactions on a broader scale could result in a dispersal limitation of certain lower-reward plant species relative to higher-reward ones and possible declines of the less preferred plant species. Ultimately, this could alter patterns of plant regeneration. Moran *et al.* (2009) showed that the plant family Rubiaceae was vulnerable to reduced dispersal due to reduced abundance of bird frugivores in subtropical Australia, and suggested that fruit chemistry may play a role in limiting the consumption of Rubiaceae to a small subset of frugivores.

Reduction of dispersal at low bird-density sites may affect recruitment in different ways. If birds remove fewer fruits, seed and seedling densities could increase under parents, with lower numbers dispersed further away than at bird-abundant sites. If there is density-dependent seed or seedling mortality under parent plants (Janzen-Connell effects: Janzen 1970; Connell 1971), reduced dispersal could result in higher seed or seedling mortality near the parent plants at low bird-density sites than bird-abundant sites. Alternatively, if there is weak or no density-dependent mortality under parents, then spatial clumping of seedlings and eventually adults may be higher in low bird-density sites than bird-abundant sites (Bleher & Böhning-Gaese 2001).

Kelly *et al.* (2004) and Robertson *et al.* (2008) suggest that as long as fruits are being removed at some point before they rot and fall below the parent plant, delays in fruit removal may have no fitness consequences. In this regard, the only plant species probably experiencing a fitness reduction is *C. areolata* at Kaituna, with 59% of the fruits taken by the end of the season, compared with nearly 100% of *M. ramiflorus* and *C. robusta* fruits. A final percent removed of 59% appears to be relatively low compared with other fruit removal studies. In one of the few New Zealand studies of

fruit removal, Kelly *et al.* (2004) monitored fruit removal over four years for two mistletoes, *Alepis flavida* and *Peraxilla tetrapetala*, at Craigieburn forest park. For both species there was no evidence of dispersal limitation with very few (<5%) ripe fruits present on plants at any one time and >90% of the total fruit crop removed by the end of the season. Herrera (1984) found total removal rates of 89-100% for seven shrub species in Spain, and in Australia the shrub *Coprosma quadrifida* had 84% of fruits removed by 14 bird dispersers (French *et al.* 1992). Therefore, it appears that *C. areolata* should be added to the list of plant species that seem to have restricted dispersal on mainland New Zealand, together with *Fuchsia excorticata*, *Rhopalostylis sapida*, and *Pittosporum crassifolium* (McNutt 1998; Anderson *et al.* 2006; Robertson *et al.* 2008). Overall however, most plant species were receiving adequate dispersal service at most forest fragments. The results suggest that plant species receive better dispersal service at high bird sites, and were consistent with the theory that low-reward fruit species suffer most when bird abundance declines.

Appendix 2.1 Example R code for Poisson GLM for bellbird counts

```
library(reshape)
birdcount12 <-read.csv("P:/Thesis/Bird counts/birdcount12.csv")
widex=cast(data=birdcount12,station +julian.day+mth+site+time
~species,value="count",fill=0,fun=mean)
longx=melt(widex)
count.sum.day=cast(data=longx,station+julian.day+mth+site+species~.,fun=c(sum,length))
names(count.sum.day)[6:7]=c("sum3","length3")
bb.all<-subset(count.sum.day, species=="bellbird")
formula=sum3~site*mth+offset(log(length3))
bb.all.glm<-glm(formula,family=poisson, data=bb.all)
anova(bb.all.glm, test="Chi")
summary(bb.all.glm)
bb.step<-step(bb.all.glm)
summary(bb.step)
```

Chapter 3: Quantifying seed dispersal by birds and possums

Rhopalostylis sapida **(nikau) seeds under a kereru roost. Photo: D. Kelly.**

Abstract

Native birds in New Zealand have declined dramatically and this has raised concern about how seed dispersal is faring, and whether introduced mammals can replace absent native birds. Possums (*Trichosurus vulpecula*) are known to eat a range of native and introduced fruits, and therefore have the potential to be important seed dispersers in New Zealand. However, little is known regarding possum seed dispersal quantity and quality compared to that of birds. To address this, I determined the relative contribution to seed dispersal by birds and possums in native forest at Kowhai Bush, Kaikoura over the 2012 autumn fruiting period. The number of seeds dispersed per hectare per day by each animal species was estimated using the number of seeds per faecal pellet, the number of faecal pellets per animal per day, and the density of animals per hectare. Faeces were collected from birds caught in mist nets, while possum faeces were collected along transects. Defecation rates were determined from observation (for birds) and from the literature (for possums). Animal abundance was determined from territory mapping and nest counts (birds), and from the number of bite marks in WaxTags; a pest monitoring device (possums). Species that consistently had high numbers of seeds per faecal sample were bellbirds (*Anthornis melanura*), silvereyes (*Zosterops lateralis*), song thrushes (*Turdus philomelos*), blackbirds (*Turdus merula*) and possums, with average numbers of seeds per sample of 11.5, 7.0, 8.3, 13.9 and 8.4, respectively. Although possum faeces contained similar numbers of seeds as bird faeces, the number of defecations per day was lower (70 for possums cf. 140 for birds). Possums were also present at lower densities than birds (1 possum ha^{-1} cf. 3 bellbirds, 3.6 silvereyes, 6.4 song thrushes, and 3.2 blackbirds ha^{-1}). Consequently, possums dispersed <3% of the total seeds, much less than bellbirds (21%), silvereyes (16%), song thrushes (33%) and blackbirds (28%). Possums also destroyed approximately 15% of seeds found in faeces, reduced the germination of gut-passed *Coprosma robusta* seed to half of that from bird faeces (30% vs. 60-70%), and did not swallow fruits any larger than those moved by the much smaller birds (c. 7 mm diameter). Consequently, there was little benefit gained from possum seed dispersal to compensate for the detrimental impacts they have on native flora directly (through herbivory) and indirectly (through predation on native dispersers).

Introduction

As a result of the worldwide declines of frugivorous animals, there is increasing need to understand the effects of disperser loss on plants (Bond 1994). Several studies have demonstrated negative impacts on seedling recruitment and plant regeneration through loss of their seed dispersers (e.g. Terborgh *et al.* 2008; Wotton & Kelly 2011). There is abundant evidence of widespread reduction of frugivores on most continents, primarily birds and mammals (Corlett 1998; Sodhi *et al.* 2004; Wright *et al.* 2007). Oceanic islands in particular have suffered from introductions of invasive species; examples include the Hawaiian and Galapagos Islands (Eckhardt 1972; Vitousek *et al.* 1987). Introduced species are now frequent in continental and island ecosystems where they make up a substantial component of the flora and fauna of most countries (Vitousek *et al.* 1997). Consequently, there is a growing body of research investigating whether introduced animals can function as effective seed dispersers and act to replace or compensate in areas where the original disperser fauna is now absent (e.g. Staddon *et al.* 2010). The negative effect of species extinctions on seed dispersal processes could be lessened if other species are able to compensate for those that have been lost (Kawakami *et al.* 2009). New Zealand's flora and fauna evolved in the absence of land mammals (apart from three species of bat) but is now home to a large number of introduced mammals, most of which are considered pests. There has been a recent call for more information about whether introduced mammals are important for seed dispersal in New Zealand (Kelly *et al.* 2010).

The common brushtail possum (*Trichosurus vulpecula*) was introduced to New Zealand from Australia in 1837 (Pracy 1974). The negative effects of possums on New Zealand ecosystems are well documented. As herbivores, possums damage native forests through selective browsing resulting in the die-back of whole canopies of trees such as *Metrosideros* spp. (rata), *Podocarpus totara* (totara), *Alectryon excelsus* (titoki), *Sophora* spp. (kowhai) and *Dysoxylum spectabile* (kohekohe) (Clout 2006). Although the foliage of common canopy species usually forms the majority of a possum's diet, they also supplement this with large quantities of native flowers and fleshy fruit when it is available, particularly in the summer and autumn (Cowan 1990). Nugent *et al.* (2000) consider possums to be 'reluctant folivores' as these non-foliar foods are an important source of energy and nutrients and more preferred than foliage. In fact, it appears that possums do poorly on a diet of only leaves, with the abundance of flowers and fruit determining their density (Nugent *et al.* 2000). In addition, possums are known to eat eggs and chicks and will even kill adult birds such as kaka (*Nestor meridionalis*), kokako (*Callaeas cinerea*) and kereru (*Hemiphaga novaeseelandiae*) (Brown 1993). Possums also suppress the fruiting of *Rhopalostylis sapida* (nikau; Cowan 1991) and *Elaeocarpus*

dentatus (hinau; Cowan & Waddington 1990) through their destruction of flowers and developing fruits. As a result, possums compete for food with native birds that disperse seeds, reducing the numbers of these birds, and disrupting this bird-plant interaction (Atkinson *et al.* 1995).

While negative effects of possum fruit consumption exist, they also have the potential to be important seed dispersers due to the wide range of fleshy fruits they eat (Coleman *et al.* 1985; Cowan 1990). Many of the seeds in fruits eaten by possums, especially larger, thin-coated ones such as *Beilschmiedia tawa* (tawa), are destroyed, but seeds of some species (especially those with thickened seed coats) pass through the digestive system intact (Clout 2006). The effect of possum gut passage on the germination of intact seeds varies widely between plant species, significantly impairing the germination of some and enhancing a few others (Williams *et al.* 2000; Dungan *et al.* 2002). Dungan *et al.* (2002) claimed that possums may be the only remaining dispersal vector for some large-seeded native species due to the reduction in numbers of large-gaped native birds such as kereru. This was disputed by Williams (2003), who argued that there is little evidence possums disperse viable seeds of large-seeded fruits greater than 10 mm diameter, and seeds up to this size are dispersed by a suite of common bird species throughout New Zealand.

Although we know that possums eat a wide range of fruit, disperse some seeds intact and some of these seeds germinate, the effectiveness of possums compared to birds as seed dispersers remains unclear and is the focus of this chapter. Understanding the relative contribution to seed dispersal made by different animal groups is a valuable part of biome research (Saba & Toyos 2003). Disperser effectiveness has both quality and quantity components (Schupp 1993). A high quality disperser consumes fruit without destroying a high proportion of seeds, and deposits viable seeds in suitable habitat for establishment, away from the parent plant. In contrast, a low quality disperser results in the loss of seeds, either through direct destruction or through deposition in unsuitable habitat for establishment. A poor quality disperser can act not only as a "sink" for the plant, but it also may reduce the crop available to high quality dispersers. A high quantity disperser removes a large number of seeds. Diet and food preferences of the dispersing animal affect the number of seeds removed, along with animal abundance.

I estimated the total animal-mediated seed dispersal in a lowland secondary forest by calculating seeds dispersed per hectare per day over the autumn fruiting period. Total seed dispersal by each animal species was calculated using three pieces of information: the number of seeds per defecation, the number of defecations per animal per day, and the density of animals per hectare. Fruit preference was determined from preference indices calculated from the proportion of a particular fruit species in the diet compared to the proportional availability of that fruit species in the forest. Seed dispersal quality was examined by comparing the proportion of damaged seeds in

faeces of different animal species, and germination of *Coprosma robusta* seeds (the most commonly sampled species) passed by different animal species. Specific questions regarding seed dispersal effectiveness were: What plant species do birds and possums disperse? What are their fruit preferences? Do possums disperse larger fruit than birds? What is the overall contribution to seed dispersal by each animal species at Kowhai Bush? Do birds or possums destroy seeds? How does the germination of possum dispersed seeds compare to that of bird-dispersed seeds? Finally, I discuss whether possum seed dispersal can compensate for bird declines and whether the benefit of possum seed dispersal outweighs the damage they cause.

Methods

Study site

This study was carried out at Kowhai Bush (173° 36' E, 42° 23' S), Kaikoura, New Zealand. Kowhai Bush is a 240 ha native kanuka-broadleaf forest, 7 km inland from Kaikoura (Fig. 3.1). The area used for this study is approximately 50 ha. Kowhai Bush has little mammalian predator control, except for some poisoning of possums around the eastern edges where the forest is adjacent to farmland. The forest canopy consists mainly of *Kunzea ericoides* (kanuka), and *Leptospermum scoparium* (manuka), with lesser amounts of *Melicytus ramiflorus* (mahoe), *Pittosporum tenuifolium* (kohuhu), *P. eugenioides* (lemonwood), *Pseudopanax arboreus* (five-finger), *Coriaria arborea* (tutu), *Dodonaea viscosa* (akeake), *Carpodetus serratus* (putaputaweta), *Griselinia littoralis* (kapuka), *Cordyline australis* (cabbage tree), and *Myoporum laetum* (ngaio). The understory is diverse, including *Coprosma* and *Rubus* species, while common ground cover species are ferns (including *Microsorum pustulatum*) and *Uncinia* species (hook sedge) (Hunt 1978; Starling-Windhof *et al.* 2011). Along its eastern margins large areas have been invaded by the introduced hedgerow species, *Berberis glaucocarpa* (barberry) and *Crataegus monogyna* (hawthorn).

The bird fauna is diverse at Kowhai Bush including native and introduced species. Common native birds present are silvereye (*Zosterops lateralis*), bellbird (*Anthornis melanura*), brown creeper (*Mohoua novaeseelandiae*), grey warbler (*Gerygone igata*), fantail (*Rhipidura fuliginosa*), South Island robin (*Petroica australis australis*) and rifleman (*Acanthisitta chloris*). Silvereyes are a recent arrival to New Zealand, thought to have self-introduced from Australia in 1856 (Heather & Robertson 2000). Common introduced birds present are song thrush (*Turdus philomelos*), blackbird (*Turdus merula*), dunnock (*Prunella modularis*) and starling (*Sturnus vulgaris*). The native shining cuckoo (*Chrysococcyx lucidus*), tomtit (*Petroica macrocephala*), tui (*Prosthemadera novaeseelandiae*), and

kereru also visit the bush (Hunt 1978). Of these birds, those that are considered major frugivores are silvereye, bellbird, song thrush, blackbird, starling, tui and kereru. Although rare in Kowhai Bush, tui and kereru are present in nearby forests, with particularly high numbers of kereru in Fyffe Palmer Reserve, just 5 km away (pers. obs.). This is presumably due to the abundance of *Prumnopitys ferruginea* (miro) fruit during the fruiting season in Fyffe-Palmer Reserve, a favoured food of kereru (Clout & Hay 1989), which is absent in Kowhai Bush.

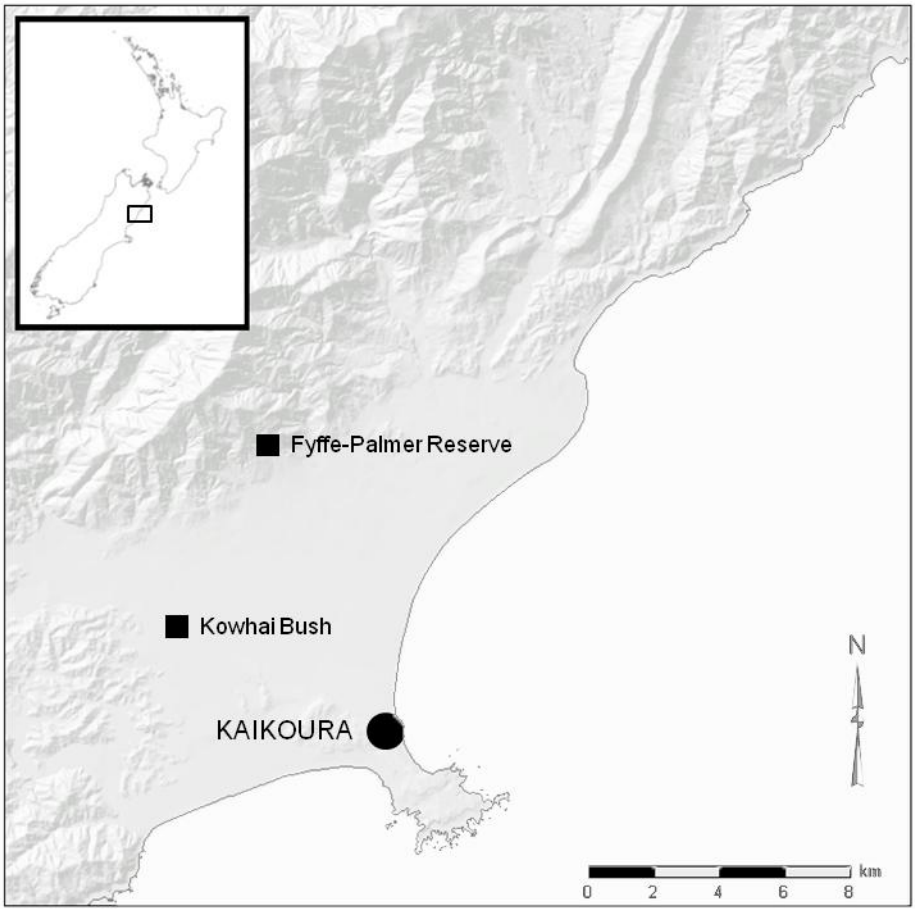

Figure 3.1 Location of Kowhai Bush in relation to Kaikoura in the South Island, New Zealand.

Seed dispersal quantity

In order to estimate the number of seeds dispersed per hectare per day, three pieces of information were required for each animal species: the number of seeds per defecation, the number of defecations per animal per day, and the density of animals per hectare.

Seeds per defecation

Bird fruit diet was examined by catching birds in mist nets to collect faecal samples. Kowhai Bush is an excellent area for mist netting forest birds because it is large, flat, clearly bounded, and partly

composed of low forest with an open interior. Mist nets with 38 mm mesh were erected in forest clearings on 30 days over autumn 2012 (March, April, May). Rigs were suspended from poles 3 m high in a similar manner to that described by Whitaker (1972). Three pole rigs were used, one 8 m long and two 12 m long. Nets were operated for approximately seven to eight hours between 0730 and 1700 hours. Sampling was restricted to fine, calm days. Nets were checked every 10 minutes. Plastic sheets one metre wide were placed below mist nets, and many birds defecated onto these sheets after they were caught in the nets. Birds were untangled within minutes and placed in cotton bird bags for 5 minutes, during which time they usually defecated. Weight, gape width, species, sex, and age were recorded. Most birds were banded before being released, to enable recaptures to be identified. Individual faeces were refrigerated before being examined for seeds under a dissection microscope. Seeds were counted and identified to the highest taxonomic level possible (in most cases to species) with the aid of a reference collection. Due to the low numbers of blackbirds and song thrushes caught, I included data collected at Kowhai Bush in the 2011 season by MacFarlane (2012) to increase sample size for the rarefaction analysis. The methods used to collect the 2011 faecal samples were identical to those used in 2012. Data that was included was from the four bird species that consistently had high numbers of seeds per faecal sample; bellbird, silvereye, song thrush and blackbird. The combined data was also used for the final estimate of seeds per faeces for these four bird species.

Possum fruit diet was examined through faecal transect sampling in Kowhai Bush. Six 200 x 10 m transect lines were initially cleared of any possum faeces in March 2012. Fresh faeces were collected from ground searches along transects over 14 days in autumn 2012 (March, April, May). Only one pellet was collected from each group of pellets found to maximise independent samples. Individual faeces were refrigerated before being examined for seeds under a dissection microscope. Seeds were counted and identified with the aid of a reference collection.

Bipartite interaction network

I used a bipartite interaction network to depict plant-disperser interactions and the relative strength of these interactions based on faecal data collected at Kowhai Bush. This was done using the "plotweb" function in the bipartite package (Dormann *et al.* 2008) for the statistical program R, version 2.15.1, which focuses on interaction webs for two trophic levels. I calculated the number of fruits dispersed using the average number of seeds per fruit, determined by counting seeds from fresh fruit, rather than presenting data on individual seeds dispersed. This is because a few plant species (particularly *Carpodetus serratus*) have many seeds per fruit and so an analysis at seed level would be dominated by these species. The bipartite interaction network included all animal species

with at least one seed in faecal samples, from the 2012 season only. The "networklevel" function was also used to analyse the bipartite network. It calculates a variety of indices including H_2', a network-level measure of specialisation that ranges between 0 (no specialisation) and 1 (complete specialisation) (Bluthgen *et al.* 2006).

Fruit preference

A preference index was calculated to determine fruit preference using fruit availability in Kowhai Bush and fruit in the diet of the animals. To estimate fruit availability, observations were made approximately every two weeks from March to May 2012, of the number and ripeness of fruit present along six 200 x 10 m transect lines. All fleshy-fruited fruiting plants present on the transect lines were recorded including species, number of fruits and percentage of ripe fruit. The number of fruits was estimated visually by dividing the plant into sections, counting the number of fruits on one section of the plant and multiplying by the number of sections on the whole plant. For small shrubs, the total number of fruits on the plant was counted. Fifteen fruit from each species were collected from at least three different plants to measure the least diameter, which determines swallowing ability of birds (Kelly *et al.* 2010). The flesh was then removed and seeds were counted and stored as a reference collection to aid seed identification.

Fruit preference of each animal species for each plant species present in the fruit survey (n = 21 plant species) was calculated for the 2012 data only, using Jacobs' (1974) food preference index (*D*):

$$D = \frac{r - p}{r + p - 2rp}$$

where *r* is the proportion of a particular fruit species in the diet, calculated using the average number of seeds per fruit, and *p* is the proportional availability of that fruit species in the forest, calculated using the maximum number of fruit present for each plant species over all fruit surveys (maximum fruit crop). Jacob's (1974) food preference index ranges from -1 to 1, where positive numbers indicate a food preference and negative numbers indicate an avoidance of a food.

Rarefaction curves

The faecal collection resulted in low numbers of samples from some important species; song thrushes and blackbirds (others have also had disproportionately low catch rates for these birds when mist netting; Williams & Karl 1996). Therefore, it was necessary to determine whether estimates of diet breadth were affected by the number of faecal samples collected. To do this I

calculated sample-based rarefaction curves (Gotelli & Colwell 2001), using the program EstimateS version 8.2 (Colwell 2009). Rarefaction curves show the increasing expected number of seed species detected with increasing numbers of faecal samples (Poulsen *et al.* 2001). I collated the faecal sample data for bellbirds, silvereyes, song thrushes and blackbirds from the 2012 and 2011 seasons. Rarefaction curves are presented for these four bird species using the collated 2011 and 2012 data, while for possums the data is from 2012 only (possum samples were not collected in 2011).

Defecations per day

I initially searched the literature for defecation rates of frugivorous birds and found only two sources, both from overseas captive birds. Cedar waxwings (*Bombycilla cedrorum*), frugivorous passerines about the size of a bellbird, have a mean defecation rate of one defecation every 2.5 min when feeding on red cedar cone and dogwood fruits (Holthuijzen & Adkisson 1984). Similarly, Graham *et al.* (1995) found mean defecation rates of one every 2.6 min for western greenbul (*Andropadus tephrolaemus*) and 2.2 min for yellow-whiskered greenbul (*A. latirostris*). I elected to conduct my own field study to obtain a more accurate defecation rate for wild birds in New Zealand that do not have constant access to food sources, by observing bellbirds in Kowhai Bush in spring 2012. Bellbirds were selected because they are a common and important mid-sized frugivore. They are also the most easily followed bird, being less disturbed by people than song thrushes and blackbirds, and do not dart around quickly as silvereyes do. Bird searches were for approximately eight hours a day between 0730 and 1900 for four days. Tracks were slowly walked and the duration of time a bird could be clearly observed and the number of defecations observed during that time was recorded.

The average number of possum defecations per night was obtained from the existing literature. Cowan (1992) trapped possums in the field and held them overnight in 12 different months. Although the number of faecal pellets excreted by individual possums was highly variable (ranging from 0-174), the monthly averages were much less variable (ranging from 59-85). The average of the monthly averages is 71.5 faecal pellets per night. Fitzgerald (1977), also trapped and held possums overnight and had a very similar average of 69.7 pellets. Similarly, feeding trials with captive possums gave an average of 71.1 pellets over a 24 hour period (Fitzgerald 1977).

Animal abundance

Bellbird abundance in Kowhai Bush was obtained from territory mapping conducted in the 2011 autumn period by MacFarlane (2012), who recorded the number of territory-holding birds in a 7.8

ha area. Since territory mapping was conducted for bellbirds only, abundance for other birds in Kowhai Bush was calculated using the number of active nests (nests with ≥ one egg or nestling) found in a 19 ha area searched in the 2002 breeding season (J.V. Briskie, pers. comm.). The number of nests per hectare was converted to birds per hectare by multiplying by two. The estimates of bird abundance gained from territory mapping and nest counts were compared to bird abundance given by Kikkawa (1966), who conducted an in-depth survey of bird populations in forest habitats of the South Island of New Zealand. The numbers used for comparison were those from low hardwood forest types and were converted from number of pairs per 100 acres to number of birds per hectare. It was known that bellbird and silvereye nests are difficult to find relative to other birds due to cryptic nest locations (J.V. Briskie, pers. comm.). Since the estimates for bellbird and silvereye abundance were low compared to those given by Kikkawa (1966), I applied an adjustment factor (×2) to correct for the cryptic nest locations of these birds. The adjustment factor also brought the bellbird estimate more in line with the estimate obtained by territory mapping. The bellbird density estimate obtained by territory mapping is conservative as it takes into account territory holding birds, but not other vagrant birds that pass through the reserve in search of food. Similarly, nest counts do not take into account unpaired or non-breeding birds. In addition, nest counts were conducted during the spring breeding season, while bird abundance would be at its peak during the autumn fruiting season when juveniles are all still alive. However, nest counts do not allow for multiple nests per pair per season, so any underestimation may be cancelled out by this.

Possum abundance was obtained by placing possum WaxTags at 20 m intervals along six 200 m transect lines in a similar method to that described by NPCA (2010). WaxTags were nailed to trees so that the wax part was 30 cm above the ground and a blaze of flour and icing sugar (5:1 ratio) was applied from the ground up to the WaxTag. WaxTags were checked for possum bite marks after three nights and the bite mark index (BMI) was calculated. Possum density was then calculated using the linear correlation between bite mark index and possums per hectare given by Thomas *et al.* (2007).

Seed dispersal quality

Germination

There has been extensive interest in whether gut passage by different animal species affects germination of the defecated seeds (Traveset & Verdu 2002; Robertson *et al.* 2006). In order to test whether there was differential germination of seeds dispersed by different animal species, seeds of the most common plant species obtained from faecal samples (*Coprosma robusta*) were sown in

trays of potting mix and placed in an unheated glasshouse. Hand-cleaned seeds of whole fruits collected from Kowhai Bush were used as a control (Robertson *et al.* 2006), with 700 control seeds in total. All seeds received at least eight weeks cold treatment in a refrigerator prior to sowing. Seedling emergence was counted at ten day intervals over the following 10 months. The probability of germination of seeds from different animal faeces was analysed using a generalised linear model (GLM), incorporating a logistic link function and binomial error distribution, using the R statistical program, version 2.15.1. *A priori* tests showed data were overdispersed, therefore, a quasibinomial error term was specified.

Results

Seed dispersal quantity

Seeds per faeces

A total of 267 birds from 12 different species were caught in mist nets in 2012 (Table 3.1). The most commonly caught frugivorous birds were silvereyes and bellbirds. Although song thrushes and blackbirds were common in the forest, low numbers were caught as they are wary of people. Only one tui was caught as they are rare visitors to the bush. Starlings were frequently seen feeding on *Pseudopanax arboreus* fruit, but caught only once and the sample contained no seeds. No kereru were seen in Kowhai Bush during the study. I collected 248 bird faecal samples and identified 1657 seeds, all of which were intact, from 24 different plant species. Of these, four plant species were not identified that were found in one faecal sample each (mostly one or two seeds), and one seed found in a bellbird sample was identified to family only (Cyperaceae). Seeds were present in the faeces of seven bird species. Three of these (fantail, brown creeper and tui) dispersed fewer than 20 seeds total, although for tui this was due to only one bird being sampled, rather than low frugivory (19 seeds in the one sample), whereas for fantails this was due to low frugivory (mean seeds per sample = 0.04). Four birds dispersed larger numbers of seeds; bellbird (597), silvereye (781), song thrush (64) and blackbird (179). Silvereyes had the highest number of plant species represented (19), perhaps consistent with having the largest number of faecal samples (see below). Blackbirds had a high number of seeds per sample of 44.8, although this was due to one sample having 132 small *Coriaria arborea* seeds. When this sample was excluded the mean number of seeds per sample dropped to 15.3. Tui had the highest number of seeds per sample, followed by blackbird and bellbird. All seeds recovered from bird faeces were intact. Pooling the 2011 and 2012 data increased the number of samples used to estimate the number of seeds per sample for the four main seed

dispersing birds (bellbird, silvereye, blackbird and song thrush) (Table 3.1). For the remainder of the chapter, data are presented for four bird species only; bellbird, silvereye, blackbird and song thrush, as these birds had a high number of seeds per sample, and the highest total number of seeds recovered.

A total of 453 intact seeds from 12 plant species were identified in possum faecal samples, with the average number of seeds per sample similar to that of silvereye and song thrush (Table 3.1). Five seeds in two possum faecal samples were identified to genus level only (*Solanum* and *Lophomyrtus*). Eight possum faeces contained seed fragments totalling 177 from two plant species. Seed fragments made up 88% of the total *Muehlenbeckia australis* seeds (100/113) and 21% of the *Carpodetus serratus* seeds (77/363). I estimated how many whole seeds the fragments made up and this was approximately 15% of the total number of seeds found in possum faeces.

Table 3.1 Seeds found in faeces of birds and possums at Kowhai Bush in 2012 (left-hand side), sorted by number of seeds per faecal sample. Right-hand columns shows collated 2011 and 2012 data. Caught is the number of individual birds caught in mist nets; not every caught bird produced a faecal sample.

	2012							2011 + 2012	
Species	Caught	Faecal sample	Samples with seeds	Intact seeds	Seed fragments	Seeds/ sample	No. seed species	Faecal sample	Seeds/ sample
Tui	1	1	1	19	0	19	2	1	19
Blackbird	4	3	3	179	0	15.3	3	13	13.9
Bellbird	48	46	44	597	0	13.0	11	80	11.5
Silvereye	106	104	90	781	0	7.5	19	194	7.0
Song thrush	10	9	7	64	0	7.1	2	14	8.3
Brown creeper	6	6	4	15	0	2.5	4	8	2.3
Fantail	57	49	1	2	0	0.0	1	63	0.0
Grey warbler	26	22	0	0	0	0	0	33	0
Chaffinch	2	2	0	0	0	0	0	5	0
Redpoll	2	2	0	0	0	0	0	2	0
Dunnock	2	1	0	0	0	0	0	4	1
Starling	1	1	0	0	0	0	0	1	0
Possum	NA	54	43	453	177	8.4	12	54	8.4
Totals	**267**	**302**	**194**	**2110**	**177**		**(28)**	**419**	

The most common seed dispersed was *Coprosma robusta* (Fig 3.2) (48% of all seeds across the whole 2012 dataset). *Coprosma robusta* made up the majority of the fruit diet for bellbirds and song thrushes, and nearly half the diet for silvereyes. *Carpodetus serratus* made up the majority of the possum diet, followed by *C. robusta*. The bipartite interaction network shows that for this sample most dispersal was of *C. robusta* by bellbirds and silvereyes (Fig 3.3). Possums had the third highest number of seeds (although they had the second highest number of faeces collected). Of the plant species that were dispersed, the average number of dispersers per fruit species was 1.90 and fruit species per disperser was 6.75. There was relatively low specialisation by birds in relation to plant seed dispersal (H_2'=0.29). Of the seeds that could be identified as native or exotic (99% of the total number of seeds), 99% were native, with *Berberis glaucocarpa* being the only exotic species dispersed. Bellbirds dispersed only native seeds, while the introduced animals plus silvereyes dispersed small numbers of exotic seeds (Table 3.2).

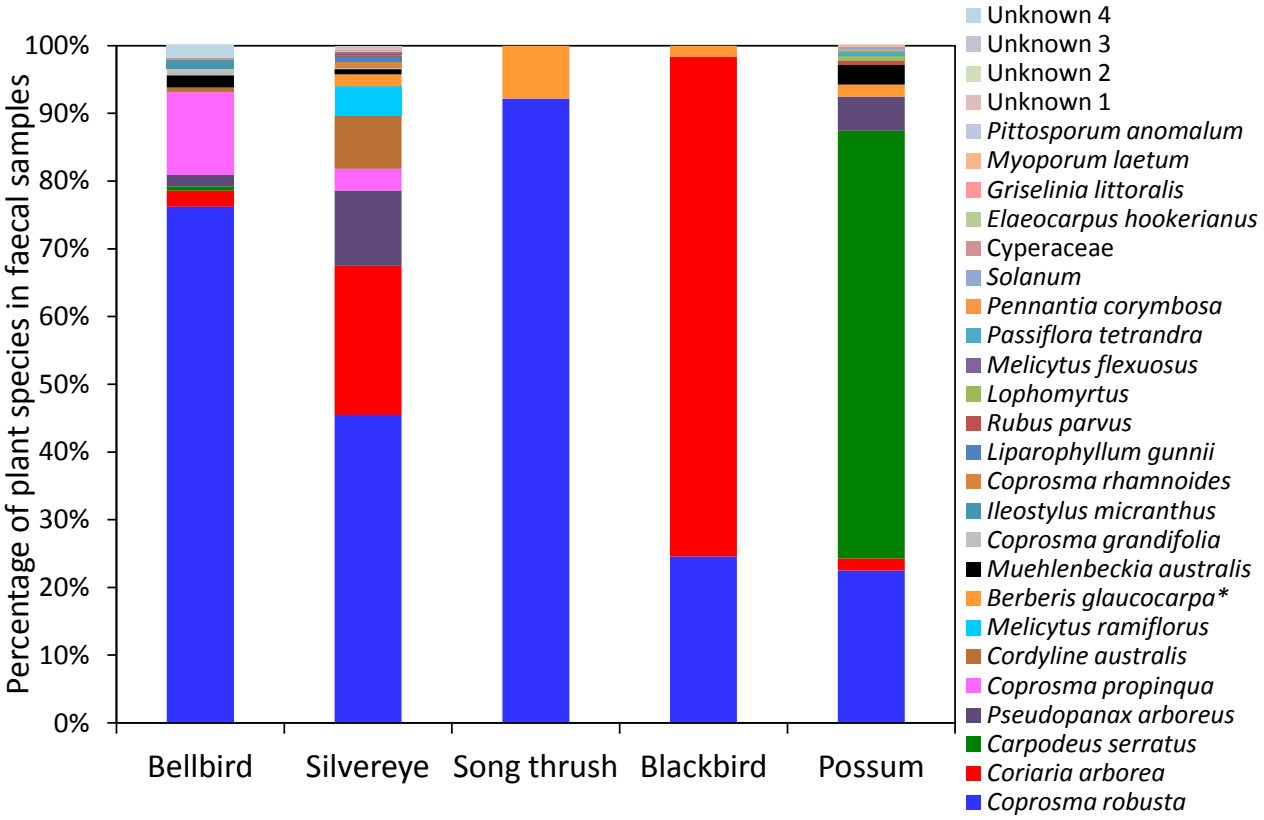

Figure 3.2 Percentage of plant seed species found in bird and possum faeces at Kowhai Bush in 2012. Plant species are ordered by increasing total number of seeds found in animal faeces. Asterisk indicates introduced plant species.

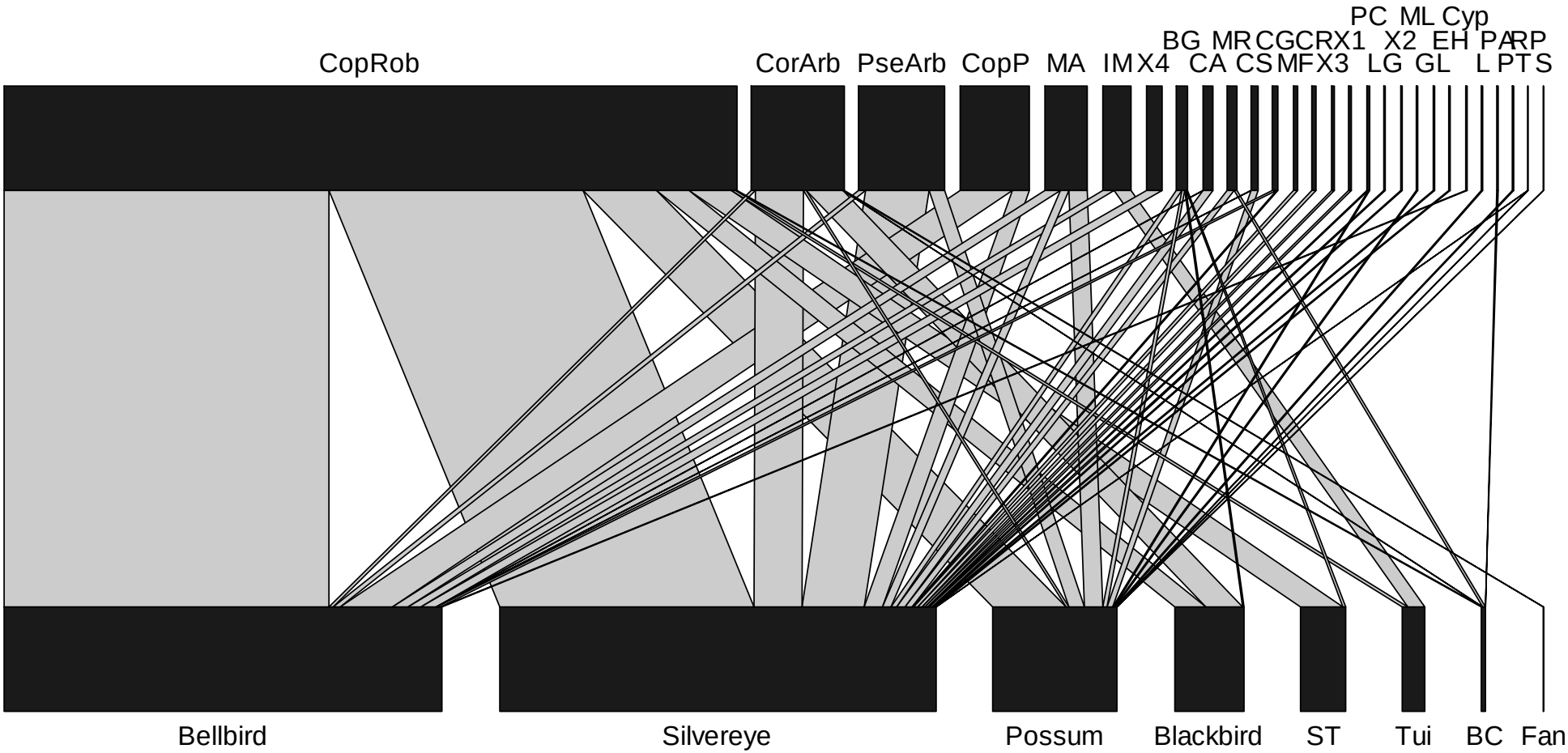

Figure 3.3 Bipartite interaction seed dispersal web showing community-level dispersal patterns for all fruit (top row) dispersed by animals (bottom row) at Kowhai Bush in 2012. The links between the bars represent an association between the plant and animal, while the thickness of the bar indicates the relative frequency of the interaction. The fruit is the unit presented here (using mean number of seeds per fruit) rather than the number of individual seeds dispersed. Abundance of animals is affected by number of faecal samples obtained, rather than relative densities of animals at the site (see text). Abbreviated bird names are ST=song thrush; BC=brown creeper; Fan=fantail. See Appendix 3.1 for full plant species list and abbreviations.

Table 3.2 Number and percentage of native and exotic seeds in animal faeces at Kowhai Bush in 2012.

Type:	Endemic	Native	Introduced			Total
Species:	Bellbird	Silvereye	Blackbird	Song thrush	Possum	
Native seeds	585	762	176	59	443	2025
Exotic seeds	0	14	3	5	8	30
Percent exotic	0	1.80	1.68	7.81	1.77	1.46

Fruit preferences

A total of 21 plant species were observed fruiting in Kowhai Bush during autumn 2012 (Table 3.3). Of these, three were exotic species (*Berberis glaucocarpa*, *Taxus baccata* and *Crataegus monogyna*). *Melicytus ramiflorus* was common in the forest but produced little fruit during the study period. Fruiting was dominated by *Coprosma robusta, Pseudopanax arboreus, Coprosma rhamnoides* and *B. glaucocarpa*. The total fruit crop was approximately 720,000 fruit per hectare, which corresponded to a seed crop of approximately 1,780,000 seeds per hectare. Although *C. robusta* was the most common fruit available, this was not the sole cause of it being the most commonly dispersed fruit as all animals had an active preference for *C. robusta,* indicated by positive Jacob's indices, while none preferred *P. arboreus, C. rhamnoides* or *B. glaucocarpa,* indicated by negative Jacob's indices (Table 3.4). *Muehlenbeckia australis* was strongly preferred by bellbirds, silvereyes and possums. Possums had a strong preference for *Carpodetus serratus*, while this was avoided by bird species. Altogether, eight plant species (making up 5.8% of available fruits) were not present in the diet of any animal during this study. Some represent plants that are highly preferred by birds not present in Kowhai Bush (e.g. kereru favour *Hedycarya arborea* (O'Donnell & Dilks 1994) and *Taxus baccata* (D. Kelly, pers. comm.)), while others were relatively uncommon so may have been detected if a larger number of samples had been collected.

Table 3.3 Fruit and seed abundance at Kowhai Bush (per hectare) and percentage of fruits in the forest (Kowhai Bush) and in the diet of dispersing animals for the 2012 season. Asterisks indicate introduced plant species. (-) indicates fruiting species not recorded in animal diets. Sorted by descending number of fruit per hectare.

Plant species	Fruit/ha	Seeds/ha	Percentage of fruits					
			Forest	Bellbird	Silvereye	Thrush	Blackbird	Possum
Coprosma robusta	287200	574400	39.9	74.3	58.3	95.6	45.2	58.8
Coprosma rhamnoides	138000	276000	19.2	0	1.0	0	0	0
*Berberis glaucocarpa**	122500	453250	17.0	0	1.2	4.4	1.7	2.5
Pseudopanax arboreus	113000	226000	15.7	1.6	14.3	0	0	13.3
Hedycarya arborea (-)	12500	12500	1.7	0	0	0	0	0
*Crataegus monogyna**(-)	8750	8750	1.2	0	0	0	0	0
Pittosporum tenuifolium (-)	7500	71250	1.0	0	0	0	0	0
Myoporum laetum	5000	5000	0.7	0	0	0	0	1.2
*Taxus baccata**(-)	5000	5000	0.7	0	0	0	0	0
Coprosma grandifolia	3500	7000	0.5	1.0	0.3	0	0	0
Ripogonum scandens (-)	3000	4200	0.4	0	0	0	0	0
Cordyline australis	2500	24750	0.4	0.1	2.0	0	0	0
Coriaria arborea	2500	12750	0.4	0.9	11.1	0	53.2	1.8
Pittosporum eugenioides (-)	2500	18500	0.4	0	0	0	0	0
Melicytus ramiflorus	1850	12136	0.3	0	1.7	0	0	0
Muehlenbeckia australis	1500	1500	0.2	3.6	2.0	0	0	15.0
Coprosma propinqua	1205	2410	0.2	11.9	4.1	0	0	0
Carpodetus serratus	1000	65200	0.1	0.0	0	0	0	5.1
Myrsine australis (-)	500	500	0.1	0	0	0	0	0
Corokia cotoneaster (-)	300	300	0.0	0	0	0	0	0
Ileostylus micranthus	300	300	0.0	2.6	0	0	0	0
Present outside transect	0	0	0	3.9	4.1	0	0	2.5
Total	720105	1781696	100%	100%	100%	100%	100%	100%

Table 3.4 Preference of birds and possums for fruit species at Kowhai Bush in 2012 (Jacob's food preference index: +1, strongly selected; -1, strongly avoided), highlighted numbers are positive, indicating a preference. Asterisks indicate introduced plant species. Sorted by descending number of fruit per hectare.

Plant species	Bellbird	Silvereye	Song thrush	Blackbird	Possum
Coprosma robusta	0.63	0.36	0.94	0.11	0.36
Coprosma rhamnoides	-1	-0.92	-1	-1	-1
*Berberis glaucocarpa**	-1	-0.88	-0.63	-0.85	-0.78
Pseudopanax arboreus	-0.84	-0.06	-1	-1	-0.10
Hedycarya arborea	-1	-1	-1	-1	-1
*Crataegus monogyna**	-1	-1	-1	-1	-1
Pittosporum tenuifolium	-1	-1	-1	-1	-1
Myoporum laetum	-1	-1	-1	-1	0.25
*Taxus baccata**	-1	-1	-1	-1	-1
Coprosma grandifolia	0.34	-0.19	-1	-1	-1
Ripogonum scandens	-1	-1	-1	-1	-1
Cordyline australis	-0.45	0.71	-1	-1	-1
Coriaria arborea	0.44	0.95	-1	0.99	0.68
Pittosporum eugenioides	-1	-1	-1	-1	-1
Melicytus ramiflorus	-1	0.74	-1	-1	-1
Muehlenbeckia australis	0.89	0.81	-1	-1	0.98
Coprosma propinqua	0.98	0.92	-1	-1	-1
Carpodetus serratus	-0.75	-1	-1	-1	0.95
Myrsine australis	-1	-1	-1	-1	-1
Corokia cotoneaster	-1	-1	-1	-1	-1
Ileostylus micranthus	0.97	-1	-1	-1	-1

Dispersal of large fruits

Despite being much larger animals, possums did not disperse larger fruits than birds. Of seeds identified in faeces, the species with the largest fruit diameter was *Coprosma grandifolia* (mean = 7.1 mm ± 0.1 SE) and this was found in both bellbird and silvereye faeces. Of seeds found in possum faeces, the species with the largest fruit diameter was *Berberis glaucocarpa* (mean = 6.6 mm ± 0.1), which was also found in silvereye, song thrush and blackbird faeces. The mean gape widths of song thrushes and blackbirds are larger than all fruits measured at Kowhai Bush (Fig 3.4). Gape width

gives a conservative estimate of swallowing ability as birds are capable of swallowing fruits with mean widths approximately 1.5 times their gape (Kelly *et al.* 2010). Possums did disperse one fruit species that was not found in bird faeces, *Carpodetus serratus*, however this fruit is approximately 6 mm, with many (mean = 65.2) small seeds (1-2 mm) and has been reported in the diet of native birds elsewhere (O'Donnell & Dilks 1994).

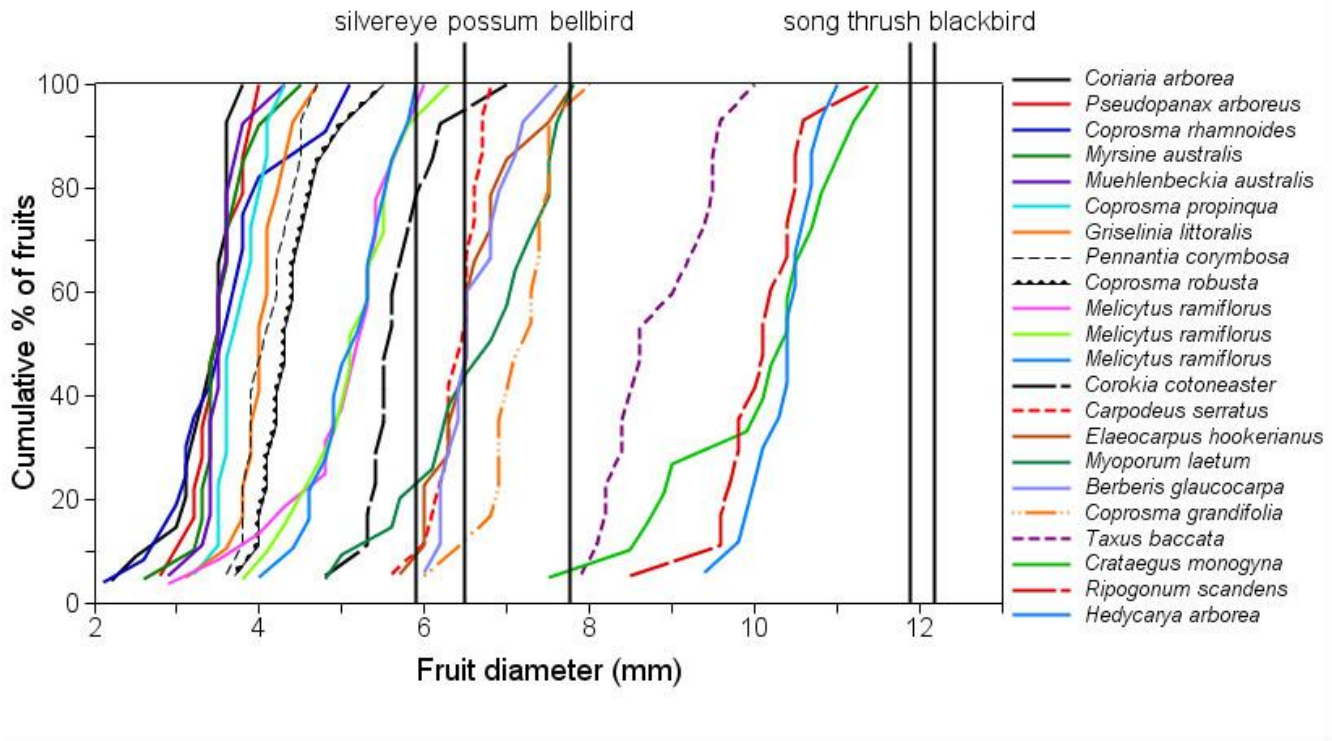

Figure 3.4 Cumulative distributions of fruit diameters for 22 fruiting plant species collected from Kowhai Bush in 2012. The mean gape width of silvereye, bellbird, song thrush and blackbird is indicated by black vertical lines and represent possible limits of consumption. The line for possums indicates the mean fruit diameter of the largest seed excreted in faeces (*Berberis glaucocarpa*). Legend shows plant species ordered by increasing mean fruit diameter.

The number of faecal samples varied widely among animal species and therefore had the potential to affect the diet breadth observed. The number of faecal samples collected for blackbirds and song thrushes was low, which made it difficult to judge how their diet breadth compared to other animals. After collating the 2012 and 2011 data, sample sizes for birds increased as follows; bellbird: 83, silvereye: 196, song thrush: 18, blackbird: 19. After rarefying back to the lowest sample size, it appeared that song thrushes and blackbirds had the lowest diet breadth: for approximately 20 faecal samples, blackbirds and song thrushes had approximately 4.8 plant species, compared to 7.8-9.5 for bellbirds, silvereyes, and possums (Fig. 3.5). However, overlapping 95% confidence intervals show that animals cannot be separated based on their diet breadth and increased sample sizes are

necessary to make conclusions about any possible differences in diet breadth. The curves show increasing slopes for most animals, suggesting that additional sampling effort would increase diet breadth, adding new seed species to the list of those dispersed in Kowhai Bush.

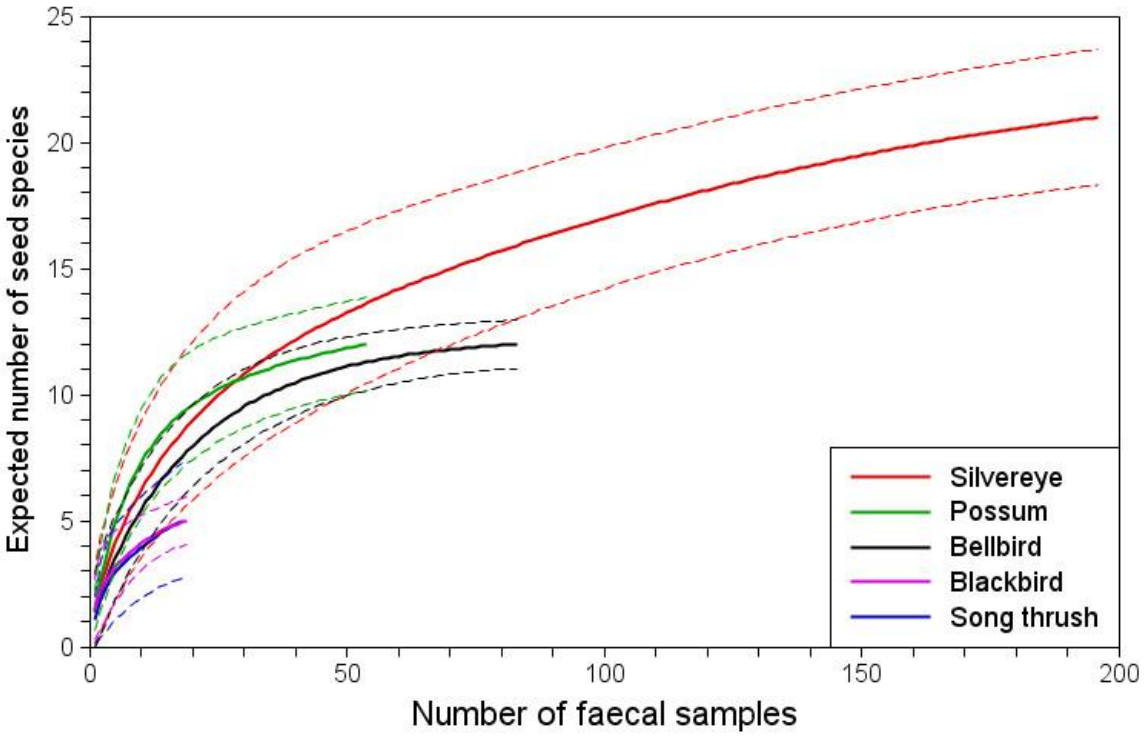

Figure 3.5 Sample-based rarefaction curves showing the expected number of seed species detected with increasing numbers of faecal samples. Dashed lines are 95% confidence intervals. Data from 2011 and 2012 seasons collated.

Defecations per day

Over the four days of bellbird observations, the total time when birds could be clearly observed was 3 hours 23 seconds in 102 sightings ranging from 5 seconds to 9:46 mins. During this time 43 defecations were observed. The data were divided into nine blocks of approximately 20 minutes each. Dividing the time by the number of defecations observed in each block gave one defecation every 4.3 ± 0.6 minutes (mean ± 95% CI). Birds were assumed to be active for approximately ten hours a day in the autumn fruiting season, so a defecation interval of 4.3 minutes over 10 hours equated to 140 faeces per bird per day. Since this is the best estimate I have for the defecation rate of frugivorous birds in Kowhai Bush I applied this to silvereyes, song thrushes and blackbirds also. As the defecation observations were conducted in spring rather than during the peak autumn fruiting season, the number of defecations per day could be underestimated due to degree of frugivory and

gut retention time being negatively associated (Levey & Karasov 1994). The number of defecations per day for possums obtained from the literature (see methods) was approximately 70.

Animal abundance

Bird abundance estimates from territory mapping and nest counts were comparable to those given by Kikkawa (1966) for low hardwood South Island forests (Table 3.4). Bellbird territory mapping revealed that 24 birds held territories in the 7.8 ha area searched in 2011, equating to 3 birds per hectare (A. MacFarlane, unpublished data). The estimate of bellbird abundance gained from territory mapping was considered to be the most accurate and this was used for calculation of total seed dispersal. For other birds, the nest count estimates were used as territory mapping estimates were not available (Table 3.4). The number of nests found in the 19 ha area searched in 2002 ranged from 11 (bellbird) to 61 (song thrush) (J.V. Briskie, unpublished data; Table 3.5). Nests per hectare were multiplied by two to give birds per hectare. After the adjustment factor was applied to the underestimated nest counts (bellbird and silvereye), the estimated number of birds per hectare ranged from 2.3 (bellbird) to 6.4 (song thrush) (Table 3.5).

Of the 60 WaxTags laid, eight were found to have possum bite marks. The BMI was calculated to be 13.3% ± 3.3 SE. This BMI equated to approximately one possum per hectare using the regression given by Thomas *et al.* (2007) between WaxTag BMI and possums per hectare.

Table 3.4 Estimates of bird abundance (birds per ha), with asterisks indicating numbers selected to use for seed dispersal calculations.

	Bellbird	Silvereye	Song thrush	Blackbird
Territory mapping	**3***	-	-	-
Nests	2.3	**3.6***	**6.4***	**3.2***
Kikkawa 1966	2.5	2.7	3.9	3.7

Table 3.5 Estimates of bird abundance at Kowhai Bush from nest counts in 19 ha of forest in the 2002 breeding season. An adjustment factor was applied to allow for cryptic nest locations (see text).

Species	Nests/19ha	Birds/ha	Adjustment factor	Adjusted birds/ha
Bellbird	11	1.2	2	2.3
Silvereye	17	1.8	2	3.6
Song thrush	61	6.4	1	6.4
Blackbird	30	3.2	1	3.2

Total seed dispersal quantity

Using the estimates of the number of seeds per defecation together with the number of defecations per animal per day and animals per hectare, I calculated total seed dispersal per hectare per day for bellbirds, silvereyes, song thrushes, blackbirds and possums (Table 3.6). Total seed dispersal by these animals was approximately 22,600 seeds per hectare per day. Dividing the total seed crop of 1,780,000 seeds per hectare (seed crop given in Table 3.3) by the number of seeds dispersed per day (22,600) equalled 79 days. This corresponded approximately to the peak fruiting period of 2-3 months over autumn. This shows that although the data uses many estimates, the numbers appear to be of the correct magnitude.

Birds contributed 97% of the total seed dispersal, while dispersal by introduced birds represented over half (60%) (Table 3.6). Blackbirds and song thrushes were much more important seed dispersers than suggested by the bipartite network. This is because the network was based on the number of samples obtained and therefore biased low for blackbirds and song thrushes, but when animal abundance was accounted for, their importance increased. Possum dispersal was less than 3% of the total seed dispersal in Kowhai Bush. Although possums had a similar number of seeds per faeces as birds, the number of defecations per day and their abundance per hectare was much lower, and as a result their seed dispersal contribution was very small.

Table 3.6 Summary of quantitative seed dispersal at Kowhai Bush, showing average seeds per defecation over 2012 and 2011 seasons, defecations per animal per day, animals per hectare, and seeds dispersed per hectare per day for the five primary dispersing animals.

	Bellbird	Silvereye	Song thrush	Blackbird	Possum	Total
Seeds defecation^{-1}	11.5	7.0	8.3	13.9	8.4	
Defecations animal^{-1} day^{-1}	140	140	140	140	70	
Animals ha^{-1}	3	3.6	6.4	3.2	1	
Seeds ha^{-1} day^{-1}	4830	3528	7437	6227	588	22610
Percentage	21.4	15.6	32.9	27.5	2.6	100

Seed dispersal quality

Germination

Seeds of *Coprosma robusta* processed by different animals varied in their germination in the glasshouse (Table 3.7a). Germination of seeds from possum faeces was significantly lower than seeds from faeces of all bird species and hand-cleaned seeds (Table 3.7b; Fig 3.6). The model was re-run without possum ingested seeds to see if the treatment effect remained, and it did not ($F_{(4, 29)}$ = 1.460, p = 0.240). The germination of *C. robusta* seeds from possum faeces was approximately 30% compared to approximately 60-70% for seeds from bird faeces (Fig 3.6).

Table 3.7a Quasibinomial GLM with germination proportion of *Coprosma robusta* seeds predicted by type of treatment applied to seeds.

Predictors	df	Deviance	F value	p value
Treatment	5	66.076	4.941	0.002
Residual	32	88.465		

Table 3.7b Quasibinomial GLM coefficients summary table for germination proportion of *Coprosma robusta* seeds predicted by type of treatment applied to seeds.

Treatment	Estimate	Standard error	t value	p value
Intercept (possum)	-0.782	0.349	-2.243	0.032
Bellbird	1.224	0.383	3.193	0.003
Blackbird	1.764	0.654	2.695	0.011
Control	1.706	0.375	4.551	<0.001
Silvereye	1.333	0.393	3.390	0.002
Song thrush	1.376	0.565	2.434	0.021

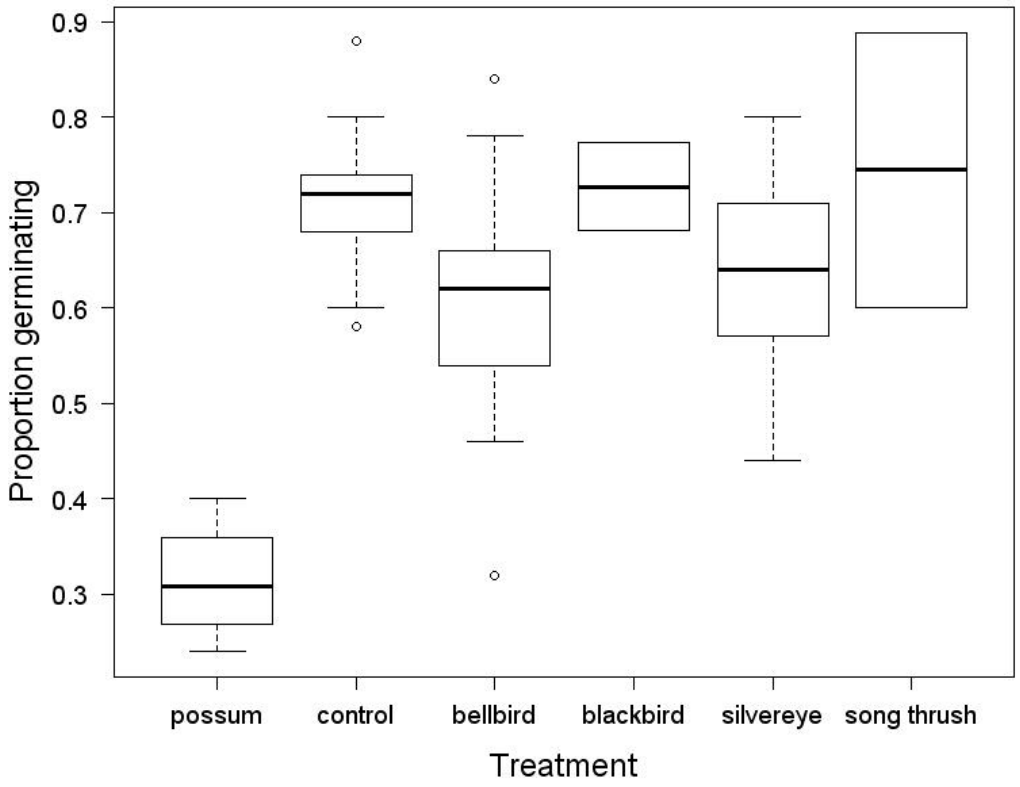

Figure 3.6 Proportion of *Coprosma robusta* seeds germinating under different types of seed treatment; passing through animal species or hand-cleaned (control). Box plot shows the median and upper and lower quartiles in the box, and minimum and maximum values in the whiskers. Open circles show suspected outliers, which are either 1.5 × interquartile range or more above the third quartile, or 1.5 × interquartile range or more below the first quartile.

Discussion

Possums made only a small contribution to seed dispersal of plants in Kowhai Bush. They dispersed less than 3% of the total seeds, compared to bird species that dispersed between 16 and 33% of the total seeds each. Furthermore, possums destroyed a proportion of the seeds they consumed, while seeds that survived gut passage intact had lower germination than bird-dispersed seeds. In addition, there was no evidence that possums fill the role of large-gaped frugivorous birds that have been lost or reduced in abundance in parts of New Zealand.

Seed dispersal quantity

Dispersers differ in the importance of fruit in their diet and this affects the number of seeds removed by the dispersing animal (Schupp 1993). I found that possum contribution to total seed dispersal at Kowhai Bush is quantitatively small relative to dispersal by bellbirds, silvereyes, song thrushes and blackbirds. Dispersal by possums was very low at Kowhai Bush partly because possums are present in low numbers. Possum abundance is variable over New Zealand and their contribution to seed dispersal may increase in areas where possums are more numerous. Possum abundance is generally lower in beech forest (ca. one per hectare) than mixed lowland forest (5-10 per hectare) reflecting the abundance of variable food sources (Clout 2006). Although possum abundance at Kowhai Bush may be relatively low, in order to make any appreciable contribution to seed dispersal possum abundance would have to be very high. If possum abundance increased to ten per hectare and bird abundance remained at the same level, possums would move 5880 seeds out of 28330 total; an increase from 3% to 21%. However, in more diverse lowland forest, higher bird densities may also be expected, which might keep the possum seed dispersal percentage the same relative to birds (unless possum predation on birds reduced bird densities).

The contribution by possums to seed rain has been described twice previously in New Zealand. In a study of alpine seed dispersal, faecal transect sampling was used to investigate the roles of introduced mammals including possums (Young 2012). However, the sampling method was unsuitable for measuring bird seed dispersal and therefore comparison between birds and possums could not be made. Dungan *et al.* (2002) sampled seed rain using seed traps in seral vegetation in lowland Canterbury and found that possums contributed 17% of the dispersed seed rain. The remaining 83% of seed dispersal was attributed to birds, although they could not distinguish between bird species. The higher contribution to seed dispersal by possums may be due to higher possum abundance and/or lower bird abundance in this seral vegetation.

Although I had small sample sizes for introduced birds (song thrushes and blackbirds), my results showed that they may be more important as seed dispersers than previously thought. Kelly *et al.* (2006) collated studies that gave the percentages of fruit visits made by all different taxa to native plants, and found that introduced birds did just 5% of fruit visits. This puts the importance of introduced birds at a much lower level than found in this study, where they moved 60% of seeds, and more than 92% of dispersed seeds were native plant species. This disparity may be due to two reasons. Firstly, the two studies use different methods. I found that song thrushes and blackbirds were regularly heard in Kowhai Bush but rarely caught due to their wariness of people, and starlings were often seen feeding on fruit in large flocks but rarely descended into the lower canopy where

the mist nets were positioned. Williams and Karl (1996) reported similar relative numbers of mist net catches per bird species to those obtained in this study. However, I was able to correct for the unequal catch rate among different bird species by using estimates of abundance. In contrast, the fruit visiting method used by Kelly *et al.* (2006) did not correct for abundance, and visits by introduced birds may have also been underestimated due to their wariness of people. Secondly, the low, shrubby kanuka-broadleaf forest of Kowhai Bush may be habitat that is better suited to blackbirds and song thrushes than the sites studied in the paper by Kelly *et al.* (2006), and therefore abundance of these introduced birds may have been higher in Kowhai Bush.

Dispersal of large fruits

One potential benefit of possums might be that they could swallow large fruits. Dispersal of the largest fruits is of concern in New Zealand, because these plant species are now largely dependent on a single frugivore (kereru) (Wotton & Kelly 2011), whose numbers are in decline in many places (Heather & Robertson 2000). However, previous work, confirmed by this study, shows that possums do not swallow any fruit larger than those swallowed by silvereyes, despite weighing about 200 times as much (2.5 kg for possums vs. 13 g for silvereyes). Silvereyes have been reported dispersing fruits up to 9.9 mm mean diameter (*Crataegus monogyna*; Williams & Karl 1996), while there is no evidence that possums disperse any fruits greater than 10 mm diameter (Williams 2003). Cowan (1990; 1992) found that possums usually eat only the skin and flesh of fruits with seeds around 10 mm and discard the seeds, including *Rhopalostylis sapida* (mean fruit diameter 9.1 mm), *Elaeocarpus dentatus* (9.2 mm), *Prumnopitys taxifolia* (9.4 mm), *Hedycarya arborea* (9.7 mm) and *Ripogonum scandens* (10.5 mm), and Williams *et al.* (2000) found the same behaviour with *Prumnopitys ferruginea* (13.0 mm) (Fruit diameters from Kelly *et al.* 2010). Cowan (1990) did find one *Ripogonum scandens* seed in possum faeces, and this appears to be the largest seed dispersed by a possum on record (although this species has variable fruit size; Kelly *et al.* 2010), however silvereyes also take this fruit (O'Donnell & Dilks 1994). In Kowhai Bush, birds and possums dispersed fruits up to approximately the same maximum size (7 mm). While possums did disperse a large number of *Carpodetus serratus,* which were not found in bird faeces, these are small fruits approximately 6 mm wide, with over 60 tiny seeds and would be well within the range of dispersal for any birds at Kowhai Bush. In fact, silvereyes, bellbirds, blackbirds and tui have all been recorded eating them elsewhere (O'Donnell & Dilks 1994). It is interesting to note that possums appeared to have fruit preferences consistent with other studies. Coleman *et al.* (1985) also found that the two most common seeds recovered from possum faeces were *Carpodetus serratus* and *Coprosma* spp.

Seed dispersal quality

Seed survival, germination

For a high quality seed disperser, there should be low seed mortality during consumption. In contrast, I found that 15% of seeds found in possum faeces were damaged and germination of *C. robusta* seeds from possum faeces was low (approximately 30%) compared to birds (60-70%). My estimate of seed damage is a minimum since I could not detect seeds that were completely digested during possum consumption. Other studies have reported similarly low values for seed survival and germination in possums. For example, Williams *et al.* (2000) showed that over a range of plant species, possums destroyed on average 66% of the seeds they consumed. Furthermore, they found that the germination percentage of *C. robusta* seeds from possums was 4%, compared with 70% for hand-cleaned seeds. Over all plant species tested, average germination was 24.7% for seeds from possums and 42.2% for controls. Dungan *et al*. (2002) reported that 75% of *Muehlenbeckia australis* seeds from possum faeces were visibly damaged and none of these intact defecated seeds germinated (compared with 40% germination in hand-cleaned seeds). I found that 88% of *Muehlenbeckia australis* seeds were visibly damaged (but did not test germination in this species). By destroying high proportions of seeds and decreasing germination, possums are probably reducing plant fitness. Since most fruits eaten by possums are also taken by birds, a fruit eaten by a possum would likely have been later eaten by a bird. Possum fruit consumption is therefore replacing a higher-quality disperser that does not reduce seed survival with a lower-quality one that does. This is analogous to the interaction between tree weta (*Hemideina* spp.) and *Fuchsia excorticata* (tree fuchsia), whereby the lack of movement and low survival rate of seeds consumed opportunistically by tree weta replaces the high-quality dispersal of birds with low-quality dispersal (Wyman *et al.* 2011).

Movement of seeds

An effective seed disperser should move seeds away from the parent plant to sites suitable for establishment. Movement of seeds was not directly tested in this study, however, we can make some inferences about likely distances seeds are moved by examining distances travelled by animals and gut passage times. Gut passage times vary with bird body size and seed size but are approximately 30 min for small to medium sized common seed dispersing birds. For example, silvereyes had a mean gut passage time of 31.5 min for *Rhagodia parabolica* (Stanley & Lill 2002) and 18 min for *C. quadrifida* (French *et al.* 1992). Tui had mean gut passage times of 33 and 40 min for

Coprosma robusta and *C. grandifolia,* respectively (O'Connor 2006). Blackbirds had gut passage times of approximately 30 min (Sorensen 1984). Kereru can have a large range of gut passage times depending on seed size; mean retention times were 37-45 min for the two smallest-seeded species (*Pseudopanax arboreus* and *Dacrycarpus dacrydioides*) and up to 109-181 min for the three largest species (*Vitex lucens*, *Beilschmiedia tarairi*, and *B. tawa*) (Wotton *et al.* 2008; Wotton & Kelly 2012). Birds can travel long distances during these long gut retention times. For example, tui, while rare in Kowhai Bush, fly on average 78 m in a single movement, with a maximum of over 2 km, and daily movements up to 30 km (Bergquist 1985). Tui disperse seeds on average 200 m (O'Connor 2006). Kereru fly on average 77 m and up to 1457 m in a single flight (Wotton & Kelly 2012). Thery (1989) radio-tracked blackbirds and one individual flew an average of 46 m in the 15 minutes following ingestion of fruit (approximately half the time required to pass most fruit). Individual blackbirds flew up to 3 km in a day between feeding zones, covering up to 16 ha.

Possums can have large home ranges (male mean 1.9 ha, female mean 1.3 ha, occasionally up to 30 ha; Green 1984; Cowan & Clout 2000) and can range widely during the course of a single night. In forest, nightly movements are generally less than 300 m, and occasionally up to 1.5 km in farmland (Clout & Efford 1984). Mean gut retention times are 1.5-3 days (Nugent *et al.* 2000). Consequently, possums too have the potential to disperse seeds over large distances. However, if there is adequate food supply within a good feeding area there may be little incentive for long distance movement. Paterson *et al.* (1995) found that possums foraged in a small area of their home range on any night, and the areas used by individuals were commonly very similar over a series of nights. The site of seed deposition is another important factor determining seed disperser quality. Possums are known to favour pasture species especially clover (*Trifolium* spp.) and grasses, and possums denning in forest will travel up to a kilometre to pasture in search of these foods (Green & Coleman 1986). Pasture species formed 12% of the diet of possums living within 300 m of the forest edge, with 90% of this being clovers and grasses (Coleman *et al.* 1985). Furthermore, possum population densities were highest at the pasture edge (Coleman *et al.* 1980). This suggests that possums will inevitably disperse some forest seeds into pasture where germination and survival will be reduced. Similarly, Young (2012), who investigated seed dispersal of New Zealand alpine plants, found that possums largely dispersed seeds from grassland/shrubland, where the fleshy-fruited species occur, into *Nothofagus* (beech) forest, which is unsuitable habitat for regeneration of most alpine plant species.

Possum impacts

Biological invasions threaten biodiversity by affecting the structure and functioning of ecosystems, altering ecological interactions that have arisen over evolutionary timescales (Traveset & Richardson

2006). Possums disrupt native plant-disperser interactions through different mechanisms. As herbivores, possums can directly affect the dispersal success of plants by consuming reproductive parts, which decreases the number of fruits available for dispersal. Possums can indirectly affect the dispersal success of plants through consumption of vegetative parts, which reduces plant population densities. This can in turn reduce bird disperser populations and cause food competition between birds such as kereru that eat leaves and disperse fruit. Possums have been shown to reduce recruitment in forests through seedling herbivory (Wilson *et al.* 2003). As predators, possums decrease the population densities of bird dispersers (Sweetapple *et al.* 2004) and thus decrease fruit visitation rates. As dispersers, possums reduce the number of seeds available for removal by more effective bird dispersers. Possums may deposit seeds in sites that are suboptimal for germination (Young 2012), destroy seeds or decrease germination percentage due to harsh gut treatment (Williams *et al.* 2000; Dungan *et al.* 2002). Possum seed dispersal behaviour may also pose a conservation risk by increasing the spread of invasive weed species. In their native country Australia, possums disperse seeds of the European weed hawthorn (Bass 1990). In New Zealand, possums are known to disperse seeds of the noxious weeds *Passiflora mollissima* (banana passionfruit) (Beavon 2007) and *Leycesteria formosa* (Himalayan honeysuckle) (Dungan *et al.* 2002), while I found that possums dispersed some *Berberis glaucocarpa* seeds. They are potentially important seed dispersers of a range of other alien species also (Williams *et al.* 2000).

Conclusion

I found that the contribution to seed dispersal by blackbirds and song thrushes was higher than previously reported and propose that they be considered more in future when studying the relative importance of seed dispersing animals. In contrast, possums were not effective seed dispersers in terms of quantity or quality, nor did they provide dispersal of large fruits. For these reasons there appears to be little benefit from possum seed dispersal of native plants to outweigh the damage they do. Birds, both native and introduced, are clearly the most important seed dispersers. There may be a fitness reduction for plants if seeds are dispersed less effectively by possums than alternative seed dispersers. Since most native fruits are eaten by birds throughout New Zealand, a fruit eaten by a possum would likely have been later eaten by a bird. Therefore, possums probably reduce the number of seeds dispersed by birds. In the complete absence of birds, possums might be useful as seed dispersers, but in the presence of birds (including silvereyes, blackbirds and song thrushes) possum fruit consumption simply replaces an effective disperser with a less effective one. Since possums both compete for resources and directly predate on birds, there are many reasons to reduce possum densities on conservation land and no reason not to.

Appendix 3.1 Species list and abbreviations for dispersed species

Species level identification codes and names (to the highest taxonomic level possible) for each seed type (n = 28) found in faecal samples to enable interpretation of the community dispersal bipartite network (see Fig 3.3). Species are ranked according to disperser richness. Unidentified species labelled as X1-4. Codes for animal dispersers (n = 8) are as follows: BB=bellbird; S=silvereye; P=possum; BL=blackbird, ST=song thrush; T=tui; BC=brown creeper; F=fantail.

Seed Code	Taxonomic name	Family	Number of dispersers	Animal dispersers
CopRob	*Coprosma robusta*	Rubiaceae	7	BB,S,P,BL,ST,T,BC
CorArb	*Coriaria arborea*	Coriariaceae	6	BB,S,P,BL,BC,F
BG	*Berberis glaucocarpa*	Berberidaceae	4	S,P,BL,ST
PseArb	*Pseudopanax arboreus*	Araliaceae	3	BB,S,P
MA	*Muehlenbeckia australis*	Polygonaceae	3	BB,P
CopP	*Coprosma propinqua*	Rubiaceae	2	BB,S
IM	*Ileostylus micranthus*	Loranthaceae	2	BB,T
CS	*Carpodetus serratus*	Carpodetaceae	2	BB,P
CG	*Coprosma grandifolia*	Rubiaceae	2	BB,S
CA	*Cordyline australis*	Asparagaceae	2	BB,S
MR	*Melicytus ramiflorus*	Violaceae	2	S,BC
PC	*Pennantia corymbosa*	Pennantiaceae	2	S,P
RP	*Rubus parvus*	Rosaceae	2	S,P
CR	*Coprosma rhamnoides*	Rubiaceae	1	S
Cyp		Cyperaceae	1	BB
EH	*Elaeocarpus hookerianus*	Elaeocarpaceae	1	S
GL	*Griselinia littoralis*	Griseliniaceae	1	S
LG	*Liparophyllum gunnii*	Menyanthaceae	1	S
L	*Lophomyrtus* sp	Myrtaceae	1	P
MF	*Melicytus flexuosus*	Violaceae	1	S
ML	*Myoporum laetum*	Scrophulariaceae	1	P
PT	*Passiflora tetrandra*	Passifloraceae	1	P
PA	*Pittosporum anomalum*	Pittosporaceae	1	BC
S	*Solanum* sp	Solanaceae	1	P
X1			1	S
X2			1	S
X3			1	S
X4			1	BB

Chapter 4: Dispersal quantity

Whole and clean *Prumnopitys ferruginea* (miro) seeds on the ground in Fyffe-Palmer Scenic Reserve, Kaikoura, New Zealand. The pink whole fruits have fallen from the tree undispersed and the brown clean seeds have passed through a bird (probably kereru). Photo: T. Wyman.

Abstract

One obvious sign of dispersal failure would be the accumulation of undispersed fruits beneath the parent tree. However, the percentage of fruits collected under parent canopies that have passed through a bird will underestimate the percentage of the total seed crop taken by birds, as many seeds swallowed by birds are dropped away from parent canopies. I investigated the relationship between percentage of fruits dispersed and distance from parent tree for three large-seeded New Zealand tree species; *Beilschmiedia tawa* (Lauraceae), *Elaeocarpus dentatus* (Elaeocarpaceae), and *Prumnopitys ferruginea* (Podocarpaceae). Over eight years, 50 m transect lines were run from the base of fruiting *B. tawa* trees into areas without *B. tawa*, and all current-season seeds on the ground were classified as clean (flesh removed by passing through a bird) or fleshed (some or all fruit pulp remaining). This method was repeated for the two other tree species in 2012. I statistically fitted 2Dt (or bivariate Student's *t*) kernels to the observed dispersal distances for fleshed and clean seeds, and then in each distance band multiplied mean seed density by the area of that annulus to allow for the larger area at greater distances from the parent tree. This allowed calculation of the percent through-bird within various maximum search distances. Dispersal kernels for all tree species showed high densities of both fleshed and clean seeds near the parent, with fleshed seeds becoming uncommon beyond 10 m, while clean seeds were present at somewhat higher densities from 10 to 50 m. Data from under the canopy were hyper-sensitive to low dispersal. I found a wide range of dispersal percentages below the canopy across years (means 22-77%), whereas when all seeds to 50 m were included, all years had between 66% and 92% of the fruit crop consumed by birds. The average percent dispersed was 81% for *B. tawa* (mean of eight years), 75% for *E. dentatus* and 91% for *P. ferruginea*. These results show that dispersal quantity below the parent tree strongly underestimates total dispersal quantity. Finding only 11-18% clean seeds under the parent tree would correspond to an overall dispersal percentage of at least 50% for all three species tested. The application of these results will help biologists and managers interpret how well dispersal mutualisms are functioning from simple measurements below parent trees.

Introduction

Due to worldwide bird declines, there is considerable interest in how well bird-plant interactions are faring, especially fruit dispersal mutualisms (Corlett 2007; Kelly *et al.* 2010). The effectiveness of animal seed dispersal depends on both the quality of dispersal (seed treatment after ingestion and quality of deposition sites) and quantity of dispersal (number of seeds dispersed) (Schupp 1993). Here, I use a novel method of assessing dispersal quantity by collecting seeds below the parent canopy and classifying them as clean (flesh removed by passing through a bird) or fleshed (undispersed whole fruits). The percentage of seeds that have passed through a bird can be used to determine seed dispersal quantity, with large percentages of whole fruits showing evidence of poor dispersal service. However, the percentage of fruits that have passed through a bird under the parent canopy will presumably underestimate the percentage of the total seed crop taken by birds, as many seeds swallowed by birds are dropped away from parent canopies (Wotton 2007). At present, the relationship between dispersal quantity below parent trees and total dispersal quantity remains unknown, and to determine it was the aim of this study.

Understanding the ecological processes that are influenced by seed dispersal requires a quantitative description of how many seeds are dispersed, and how far from the parent plant they are taken (Westcott 2007). The quantity of seeds dispersed is an important aspect of seed dispersal, since it gives an indication of how well the interaction is faring in the presence of bird declines. Dissemination limitation occurs when frugivore activity limits the number of seeds successfully dispersed away from parent trees, independent of the quantity of seeds produced by the plant (Jordano & Godoy 2002). There is extensive evidence of widespread human-caused frugivore declines (primarily birds and mammals) on most continents (Sekercioglu *et al.* 2004; Wright *et al.* 2007). This can lead to effects on plant recruitment through the loss of services provided by seed dispersing animals such as facilitating germination, enabling escape from seed predators, increasing gene flow, and enabling colonisation of new sites (Sekercioglu *et al.* 2004). There is particular concern for the dispersal of large-seeded plant species, which are inherently more vulnerable to dispersal failure. This is because gape size tends to limit the size of fruit an animal can swallow (particularly for birds), so fewer animals are capable of dispersing large-seeded plant species. Furthermore, declines of large-bodied frugivores are well documented as they tend to have lower population densities, slower life histories, larger home ranges, and are more likely to be hunted, which are all factors that make them more vulnerable to human activity (Roff & Roff 2003; Schipper *et al.* 2008; Boyer 2010).

Concern is sometimes raised about the need for seeds to pass through a frugivore's gut in order to germinate, enhanced by removal of the fruit pulp or scarification of the seed coat. However, experimental evidence suggests that this 'scarification effect' is usually small (Robertson *et al.* 2006; Traveset *et al.* 2007; Kelly *et al.* 2010). Perhaps more important is the transport of seed away from the parent plant. The frequency distribution of dispersed seeds relative to distance from a parent plant has been termed the dispersal curve or kernel (Levin *et al.* 2003). Experimental and theoretical research suggests that the initial spatial distribution of dispersed seeds plays an important role in determining the structure and dynamics of plant populations and communities (Nathan & Muller-Landau 2000; Levine & Murrell 2003). The pattern of seed dispersal serves as a template for subsequent processes such as germination, predation, competition and survival, all of which can ultimately affect the spatial distribution of adult plants (Schupp & Fuentes 1995). Seeds that disperse over relatively short distances typically have lower survival than those that disperse further away from conspecifics. The escape hypothesis, first proposed by Janzen (1970) and Connell (1971), proposes that seed dispersal reduces density-dependent mortality of seeds and seedlings by allowing escape from competitors, seed predators, pathogens, and herbivores. Since seed density generally decreases away from parent plants, seed dispersal can improve survival chances by reducing competition between seedlings (Herrera 2002). This density-dependent mortality was believed to be important in tropical forests but not temperate ones due to higher abundances of natural enemies and a greater degree of natural enemy specialisation in aseasonal tropical habitats (Janzen 1970). However, an increasing number of studies have demonstrated Janzen-Connell effects in temperate plant species (Packer & Clay 2000; Fitzsimons & Miller 2010; Martin & Canham 2010; Wotton & Kelly 2011). HilleRisLambers *et al.* (2002) found that the proportion of species affected by density-dependent mortality is equivalent in temperate and tropical forests.

Island archipelagos of the Pacific have suffered from the recent wave of alien introductions brought by people, resulting in species extinctions and declines. In New Zealand, human settlement and the introduction of mammalian predators had a huge impact on the bird fauna, leading to extinction of 41% of endemic forest bird species (Innes *et al.* 2010). Others are functionally extinct (sensu Sekercioglu *et al.* 2004) and persist only in small isolated sanctuaries, for example, kokako (*Callaeas cinerea*), hihi (*Notiomystis cincta*) and saddlebacks (*Philesturnus carunculatus*). Dispersal of fleshy fruits in New Zealand is now almost entirely dependent on four native birds; silvereyes (*Zosterops lateralis*), bellbirds (*Anthornis melanura*), tui (*Prosthemadera novaeseelandiae*) and kereru (*Hemiphaga novaeseelandiae*) (Kelly *et al.* 2006). Furthermore, dispersal of five large-seeded tree species (fruit width greater than 14 mm) is now largely dependent on the kereru, whose numbers have decreased since human arrival (Clout & Hay 1989; Innes *et al.* 2010). Consequently,

large-seeded trees in New Zealand are vulnerable to dispersal failure. However, as for most bird-dispersed plants, there is little information on the actual current levels of dispersal quantity.

The few studies of dispersal quantity of New Zealand plant species have found varying levels of dispersal service (Kelly *et al.* 2010). Most of these studies use the rates that fruits were removed from plants, or the percentage of fruits on tagged branches that had time to go overripe before being removed by dispersers (e.g. Kelly *et al.* 2004; Robertson *et al.* 2008). Studies of overseas dispersal quantity are relatively rare and are usually designed to describe the spatial distribution of dispersed seeds, but rarely mention fruits that fall to the ground undispersed (Hoppes 1988, Kitajima and Augspurger 1989, Laman 1996, Clark et al. 1999). I am not aware of any studies that classify seeds as clean or fleshed to determine percentages of bird-dispersed seeds, perhaps because in many countries, vertebrate seed predators rapidly harvest seeds off the ground to consume or bury them.

In this paper I investigate dispersal quantity in relation to distance from the parent tree. Specifically, I measure the relationship between distance and percentage of fruits dispersed, and whether dispersal quantity below the parent tree is a reasonable estimate of total dispersal. I define dispersal quantity as the percentage of seeds that have passed through a bird, and test this in three large-seeded New Zealand trees in native forest reserves.

Methods

Study species

Beilschmiedia tawa (A.Cunn.) Benth. et Hook. f. ex Kirk (tawa, Lauraceae) is endemic to New Zealand and is one of about 270 species of the mainly tropical genus *Beilschmiedia* (Poole & Adams 1994). *Beilschmiedia tawa* is an evergreen tree that reaches 30 m tall and is one of the major canopy-forming species of lowland forests in the North Island and the north of the South Island (Knowles & Beveridge 1982). The fruit are large single-seeded drupes (fruit 30.9 x 17.3 mm, seed 24.8 x 10.9 mm; Burrows 1999b) that are dispersed primarily by kereru (Kelly *et al.* 2010).

Elaeocarpus dentatus (J.R. et G Forst.) Vahl. (hinau, Elaeocarpaceae) is one of three endemic species in the Elaeocarpaceae family in New Zealand. *Elaeocarpus dentatus* is an evergreen tree, reaching around 20 m tall, and a lowland species found in forests up to 600 m throughout much of the North and South Islands. The fruit are purplish single-seeded drupes (mean fruit diameter 9.2 mm; Kelly *et al.* 2010).

Prumnopitys ferruginea (D. Don) Laubenf. (miro, Podocarpaceae) is a tall (up to 35 m), endemic podocarp tree, widespread in forests throughout New Zealand from sea level to c. 600 m. *Prumnopitys ferruginea* produces reddish-pink, drupaceous "fruits" around 13 mm in diameter (Kelly *et al.* 2010), consisting of a fleshy exocarp surrounding a large "seed" with a woody endocarp encasing the endosperm (Clout & Tilley 1992). Botanically, this entire structure is a seed, but functionally and ecologically it is a fruit and will be referred to as such. In autumn and early winter, ripe *P. ferruginea* fruits are an important food of kereru (McEwen 1978).

Study sites

Dispersal quantity of *B. tawa* was monitored at Blue Duck Scientific Reserve (42°14'S, 173°47'E, 430 m elevation), 20 km north of Kaikoura in the South Island of New Zealand, near the southern distribution limit of this species (Fig 4.1). The forest canopy in this 152 ha reserve is dominated by emergent *Dacrydium cupressinum*, *Prumnopitys taxifolia* and *Podocarpus totara*, with lesser amounts of *Dacrycarpus dacrydioides* and *P. ferruginea*. Common species in the subcanopy are *E. dentatus*, *Melicytus ramiflorus*, and *Hedycarya arborea*, along with localised dense patches of *B. tawa* (Hurst *et al.* 2002).

Elaeocarpus dentatus and *P. ferruginea* were monitored at Fyffe-Palmer Scenic Reserve (42°22'S, 173°38'E, 245 m elevation), 11 km south of Blue Duck Reserve (Fig 4.1). The forest canopy in this 70 ha reserve is similar to that of Blue Duck Reserve, except that *B. tawa* is absent.

Birds present at Blue Duck Reserve that have been reported to eat *B. tawa* fruit are kereru and tui (Booth 1984; Clout & Hay 1989). Birds present at Fyffe-Palmer Reserve that have been reported to eat *P. ferruginea* fruit are kereru, tui, bellbird and blackbird (*Turdus merula*) (Clout & Hay 1989; O'Donnell & Dilks 1994), and the only birds present known to take *E. dentatus* fruit are kereru (Clout & Hay 1989). There is no management in Blue Duck Reserve of introduced mammalian pests such as ship rats (*Rattus rattus*), feral cats (*Felis catus*), brushtail possums (*Trichosurus vulpecula*) and stoats (*Mustela erminea*), and only low-intensity management at Fyffe-Palmer Reserve. Red deer (*Cervus elaphus*), pigs (*Sus scropha*) and goats (*Capra hircus*) are occasionally present in Blue Duck Reserve but apparently absent at Fyffe-Palmer. There is no evidence of seed caching by mammals in New Zealand (Wilson *et al.* 2007), so seed predation usually leaves signs, and I believe it was uncommon at my sites. *Beilschmiedia tawa* seeds are unpalatable to rats, but are eaten by possums and pigs (Knowles & Beveridge 1982). Rats chew into *P. ferruginea* and *E. dentatus* fruits, leaving characteristic tooth marks (Beveridge 1973; Wilmshurst *et al.* 2008), but I saw little evidence of this.

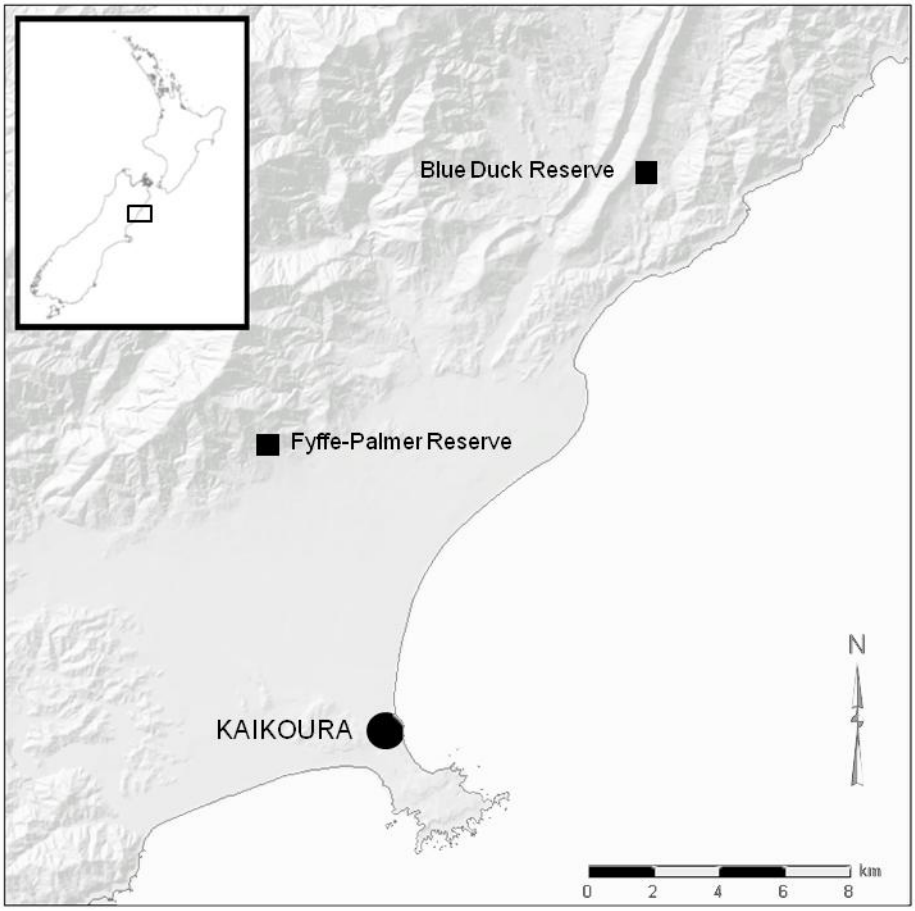

Figure 4.1 Location of Blue Duck Reserve and Fyffe-Palmer Reserve in relation to Kaikoura in the South Island of New Zealand.

Dispersal in *B. tawa*

Beilschmiedia tawa provides a useful model system to measure dispersal distances by hand-searching because it has a fruit large enough to be obvious on the forest floor, fruits only last one year so I could be certain that only current-season seeds were counted, and there is little removal of fruit from the ground by vertebrates. Also, the plant has a clumped and patchy distribution in Blue Duck Reserve, enabling us to move away from fruiting trees without getting close to another conspecific tree. In eight seasons since 1994, dispersal quantity of *B. tawa* fruits by birds was monitored along 50 m transect lines. On 1-2 days in the middle of the fruiting season (usually April), 50 x 1 m transect lines were run from the base of mature *B. tawa* trees on the edge of the *B. tawa* patch, in a direction that did not take them near to another fruiting *B. tawa* tree. All current-season fruits on the ground were classified as clean (flesh removed by passing through a bird) or fleshed (at least some fruit pulp remaining). The number of transect lines per year varied between 8 and 18 (Table 1). Most transects ran downhill, at slopes of around 10-15%.

To check whether collecting seeds off the ground might bias the apparent fraction dispersed, I compared the percentage of clean *B. tawa* seeds off the ground in the 0-5 m distance with the percentage of clean *B. tawa* seeds collected in seed traps that are maintained in Blue Duck Reserve for another study. The seed traps are under *B. tawa* trees, monitoring 10 trees from 2004 - 2011, and increasing to 15 trees thereafter. I had transect data for seeds off the ground in five of those years (2005, 2007, 2008, 2011, 2012), and in 2004 had data for seeds collected off the ground using a comparable method to the transects, in 10 plots of 1 m^2 (one per seed trap tree). The percentage of clean seeds in seed traps and off the ground were significantly correlated ($r = 0.8306$, $df = 4$, $p = 0.041$), showing that the results were not sensitive to selective removal of some seeds off the ground by animals. Furthermore, in 2012, *B. tawa* seeds (nine groups of 5 clean and 5 whole fruits per group) were tagged with nylon line and left on the ground overnight for one night to record the percentage of seeds that were removed by vertebrates, but none of the 90 seeds were disturbed despite it being a low-seed crop year.

Dispersal in *E. dentatus* and *P. ferruginea*

To see if the same pattern of dispersal quantity held for other species, dispersal quantity was determined in the same manner for *E. dentatus* and *P. ferruginea* in one season (2012) at Fyffe-Palmer Reserve. Ten transects for each species were monitored. In contrast to *B. tawa*, seeds of *E. dentatus* and *P. ferruginea* can persist intact on the forest floor for more than one year, so the lines were cleared of any seeds a few months prior to fruit ripening and measurement of dispersal quantity.

Dispersal modelling

Dispersal is summarised by a seed shadow, which is modelled as the product of a plant's fecundity *Q* and a dispersal kernel *f.* Inverse modelling is a powerful methodology for estimating fecundity and dispersal (Ribbens *et al.* 1994; Clark *et al.* 1998). The approach uses the spatial pattern of seed recovered from adult trees to statistically estimate the seed shadow. I followed Clark *et al.* (1999) in assuming that fecundity is proportional to basal area *b*. Since basal area was not measured and seed crops varied among years, parameter *b* corresponds to the product of beta, basal area and a year effect given in Clark *et al.* (1999):

$$Q(b) = \beta b$$

Among all families of dispersal kernels I chose the 2Dt function (or bivariate Student's *t*) described by Clark *et al.* (1999):

$$f(r) = \frac{p}{\pi u \left(1 + \frac{r^2}{u}\right)^{p+1}}$$

where *r* is the distance from the tree, *u* is a scaling parameter and *p* is a shape parameter. Hence *p* and *u* are parameters to be estimated. This composite dispersal function assumes a range of dispersal patterns, both local and long distance. The 2Dt curve is well suited for seed dispersal studies and fits dispersal data better than do the traditional exponential or Gaussian kernels (Clark *et al.* 1999). The 2Dt kernel becomes Gaussian when the shape parameter *p* becomes large, and Cauchy when *p* tends towards zero (Clark *et al.* 1999). I thus assumed that the observed number of seeds at distance *r* from the tree is a realisation of a Poisson process with mean $\mu(r)$:

$$Y \sim Poisson(\mu(r))$$

The mean is equal to:

$$\frac{b * p * n}{\pi u \left(1 + \frac{r^2}{u}\right)^{p+1}}$$

where *b*, *p* and *u* are the parameters to be estimated and *n* is the number of transects.

The model was fitted within a hierarchical Bayesian framework using WinBUGS 1.4 (Lunn *et al.* 2000). The parameters *b* and *u* were given uniform priors between 0 and 10^7, while the parameter *p* was given a uniform prior between 0.5 and 10, following the recommendations by Clark *et al.* (1999). Some sensitivity analysis was done by extending the limits of the uniform prior of *p* to 0.1 and 100, without effect on the resulting estimates. I monitored 5000 iterations after 5000 iterations were discarded as a burn-in. The convergence was assessed visually. To compare alternative models fitted to the same data, I used the Deviance Information Criterion (DIC, Spiegelhalter *et al.* 2002). Like the Akaike Information Criterion (AIC) used in classical statistics, DIC trades off model fit against model

complexity, with lower DIC values indicating better model performance. I compared models that allowed all parameters to vary with year and seed type, to those that fixed *p* and *u* common to seed type and only allowed *b* to vary with year. The year-specific 2Dt model had a much lower DIC (7169) than the model that fixed *p* and *u* common to seed type (9326), meaning that there was enough between-year variation in shape to have to take that into account. The seed type-specific expected 2Dt curves were then produced by model averaging across the years.

In order to estimate the total number of seeds within the radius *R* from the parent tree, the mean estimated counts per m^2 at distance *r* from the tree were multiplied by the area of the corresponding annuli and the results summed up:

$$\mu_{total} = \sum_{r=1}^{R} \mu(r)(2r-1)\,\pi$$

The percentage of bird-dispersed seeds was then evaluated by dividing the total number of clean seeds by the total number of clean and fleshed seeds. I defined the percentage of clean seeds over the entire 50 m transect, after correcting for area around the tree, as the true percentage of bird-dispersed seeds. To model the effect of variable true percentages on the estimates I used posterior simulation as follows. For postulated values p = 5, 15, ... 95%, I scaled the estimated model-averaged curves accordingly and used them to generate counts from a Poisson distribution with mean $\mu_{ave}(r)$ for each seed type. I then used the resulting counts to estimate the percentage. The posterior simulations were run in R version 2.15.1, and were based on samples from the posterior distribution of $\mu_{ave}(r)$ produced by WinBUGS. The WinBUGS and R code is given in Appendix 4.1 and 4.2, respectively.

Results

Over the eight years (1994, 1997, 2003, 2005, 2007, 2008, 2011, 2012), 91 *B. tawa* transects were searched (4550 m^2) and 10,649 *B. tawa* seeds were found (Table 4.1). No transects were run in very low fruiting years, but the sampled years ranged from modest to high seed density. Over the eight years the mean distance moved for fleshed seeds was 5.8 m, while for clean seeds it was 14.0 m. Movement of *E. dentatus* and *P. ferruginea* seeds was similar to that of *B. tawa*; the mean distance

moved for *E. dentatus* and *P. ferruginea* fleshed seeds was 4.6 and 4.7 m, respectively, and for clean seeds 11.8 and 14.7 m, respectively.

Table 4.1 Forest floor seed densities under the canopy (< 5 m of the trunk), seed crops, and dispersal data for *Beilschmiedia tawa*, *Elaeocarpus dentatus* and *Prumnopitys ferruginea* from 1 x 50 m transects.

Species	Year	n transects	n seeds found	Seeds m^{-2} (<5 m dist)	Median distance fleshed (m)	Median distance clean (m)
B. tawa	1994	11	4451	64.4	2	3
B. tawa	1997	14	689	3.8	7	15
B. tawa	2003	8	403	5.0	5	6
B. tawa	2005	9	401	5.3	3	5
B. tawa	2007	18	795	5.8	3	5
B. tawa	2008	15	2169	18.3	3	18
B. tawa	2011	8	1496	15.1	3	13
B. tawa	2012	8	245	2.6	2	16
E. dentatus	2012	10	2044	21.7	4	7
P. ferruginea	2012	10	1952	15.2	4	10

Dispersal modelling

The 2Dt dispersal kernels fitted the observed data well for all three plant species (Fig 4.2). The mean 2Dt dispersal kernels for all three tree species showed high densities of both fleshed and clean seeds near the parent, with fleshed seeds rapidly becoming uncommon beyond 10 m, while clean seeds declined more gradually with distance (Fig 4.2). Using the area-corrected modelled estimates, 48% of fleshed *B. tawa* seeds and 11% of clean seeds were found under the canopy (0-5 m), with the rest (52% of fleshed seeds and 89% of clean seeds) beyond 5 m. This was similar for *E. dentatus* (43% of fleshed and 11% of clean seeds found within 5 m) and *P. ferruginea* (42% of fleshed and 6% of clean seeds found within 5 m). Of the total seed crop (fleshed plus clean), 60-78% were dispersed beyond 10 m for all species.

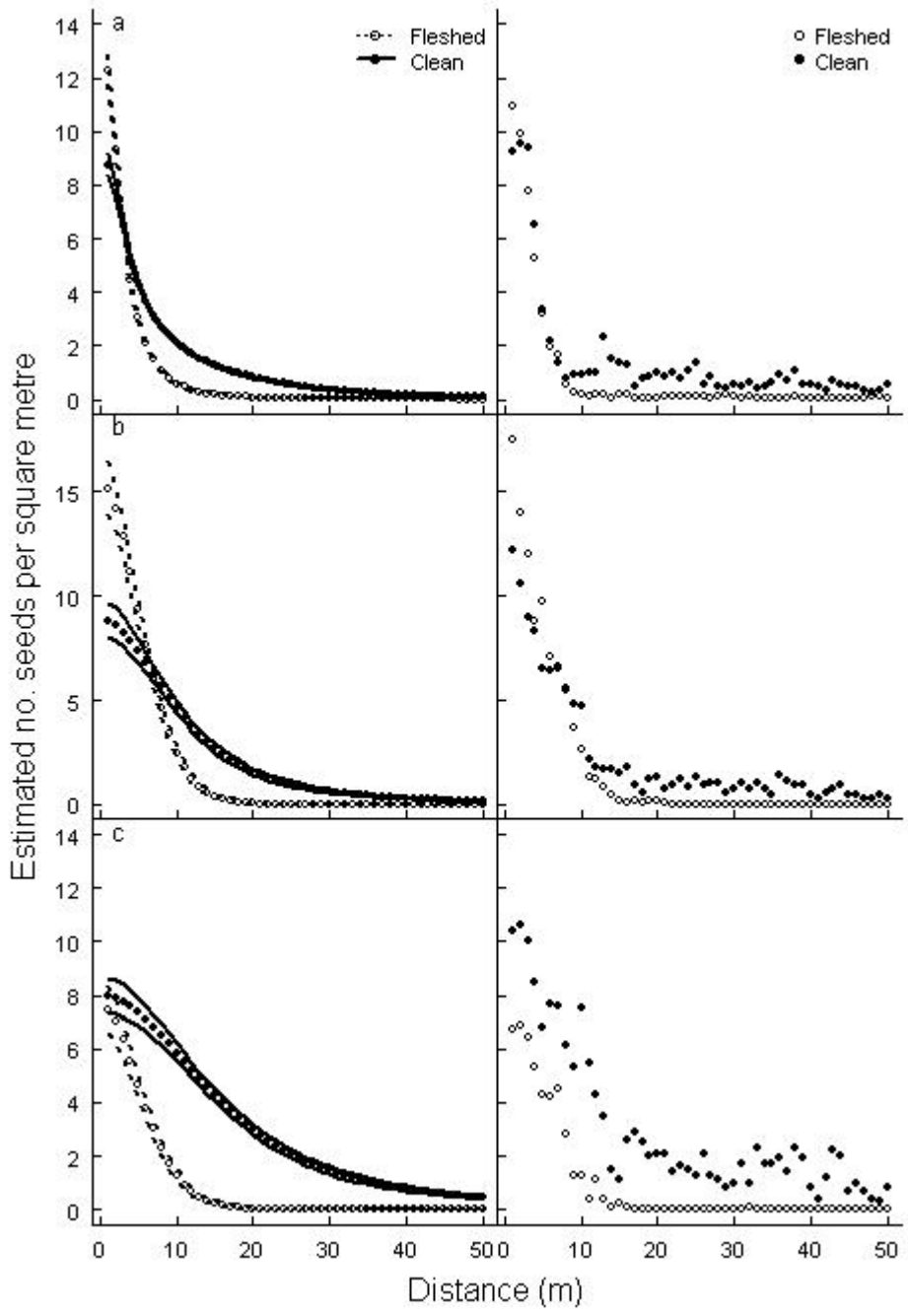

Figure 4.2 Average seed density m^{-2} out to 50 m from parent for fleshed (whole: hollow symbols) and clean (through bird: filled symbols) seeds. a: *Beilschmiedia tawa* (mean of eight years), b: *Elaeocarpus dentatus*, c: *Prumnopitys ferruginea*. Left column: fitted 2Dt dispersal kernels (means with 95% credible intervals). Right column: observed seeds per m^2.

The estimated seed totals at each distance (allowing for area) in each year and for each tree species were used to calculate the percentage of seeds that had been through a bird within various search radii (Fig 4.3). This analysis confirmed that larger search radii included more seeds from further away that were overwhelmingly clean, increasing the total percent clean. The slope of this effect varied among the eight years for *B. tawa*. For this species, in the 0-5 m band, an average of 53% of seeds

had been through a bird, with a range over the eight years of 22-77%. However, when all seeds out to 50 m radius were included, 66-92% of the fruit crop was consumed by birds (Fig 4.3a). Increasing the search radius usually increased the percent clean greatly, although least so in 1997 (the second-lowest seed crop), when the total number of fleshed seeds found was low, and a group of fleshed seeds was recorded at 15-16 m distance. That was the only year when the median distance moved by fleshed seeds exceeded 5 m (Table 4.1). The average dispersal quantity of *B. tawa* for all eight years over the 50 m radius was 81%. Dispersal quantity of *E. dentatus* over the 50 m radius was 75%, while *P. ferruginea* had the highest mean at 91% (Fig 4.3b).

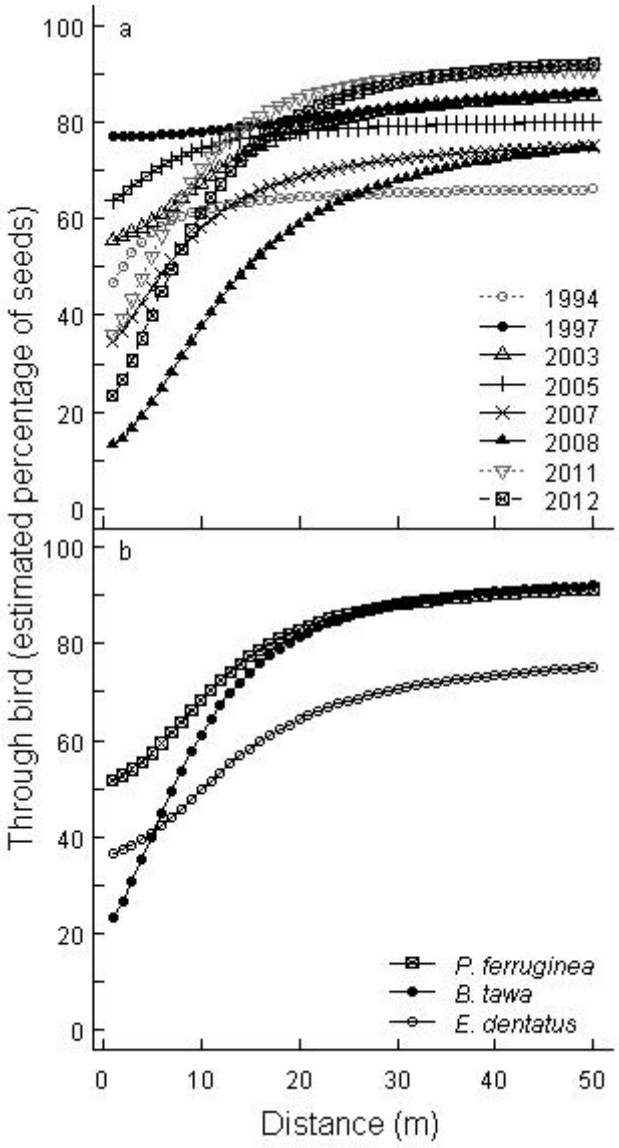

Figure 4.3 Estimated percentage of total seed crop consumed by birds as a function of search distance away from the parent tree. a: *Beilschmiedia tawa* over eight years, b: *Prumnopitys ferruginea*, *B. tawa* and *Elaeocarpus dentatus* in 2012. Each point is the percentage of clean seeds for all seeds within the listed maximum radius, i.e. the 3 m radius includes the seeds within 1, 2 and 3 m, etc. Seed totals are corrected for the increasing area of annuli with increasing radius from the parent tree.

As I had no years in which the overall percentage consumed fell below 66%, I modelled the effects of lower bird densities for *B. tawa* (modelled as a variable percentage of the whole seed crop consumed by birds), using the mean dispersal kernels for whole and clean seeds from Fig 4.2a. Limiting the search radius close to the tree underestimated percent dispersed (Fig 4.4), and the underestimation was particularly obvious at short search distances and intermediate true percentages. Even so, underestimation was found throughout the range of true percentages. For *B. tawa* a true percent dispersed of 95% equated to an under-canopy measurement of 78%, the latter representing a four-fold overestimate of undispersed fruits (22% undispersed vs. 5%). Similarly, a true percent of 85% equated to 53% under the canopy, which implies that even 50% dispersed under the canopy corresponded to very good overall dispersal. At low true percentages the underestimation was absolutely smaller but still large in relative terms. For example, for *B. tawa* at a true 10% clean, the under-canopy estimate was 2.1%, only one-fifth of the correct value. The patterns for *E. dentatus* and *P. ferruginea* were similar to *B. tawa* (Fig 4.5). To have less than 50% dispersal of the whole seed crop, for all three tree species, the under-canopy estimate had to be below 20% (17% for *B. tawa*, 11% for *P. ferruginea*, and 18% for *E. dentatus*: Fig 4.5).

Therefore, data from under the canopy were hyper-sensitive to low dispersal quantity. A high percentage consumed under the canopy always indicated good dispersal, but a low percentage consumed under the canopy could occur when the majority of the whole seed crop was consumed.

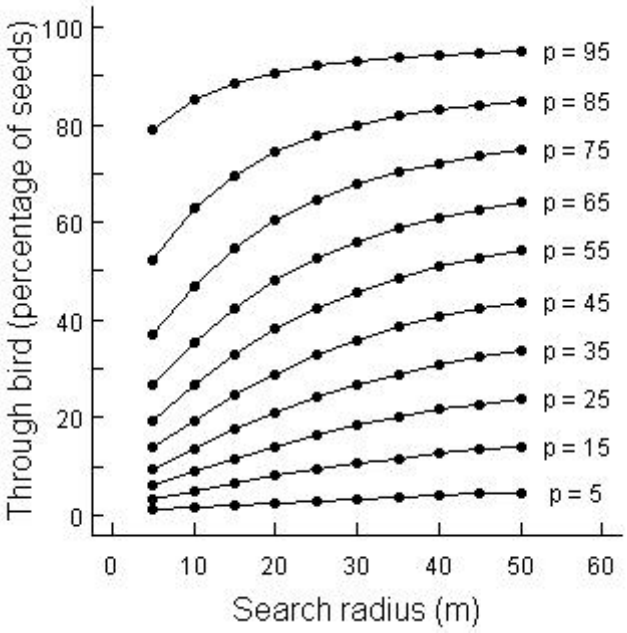

Figure 4.4 Modelled apparent percentage (measured under canopy) of *Beilschmiedia tawa* seed crop consumed by birds, as a function of search radius, where the true percentage consumed of all seeds within 50 m of the parent is fixed (5, 15, .. 95%).

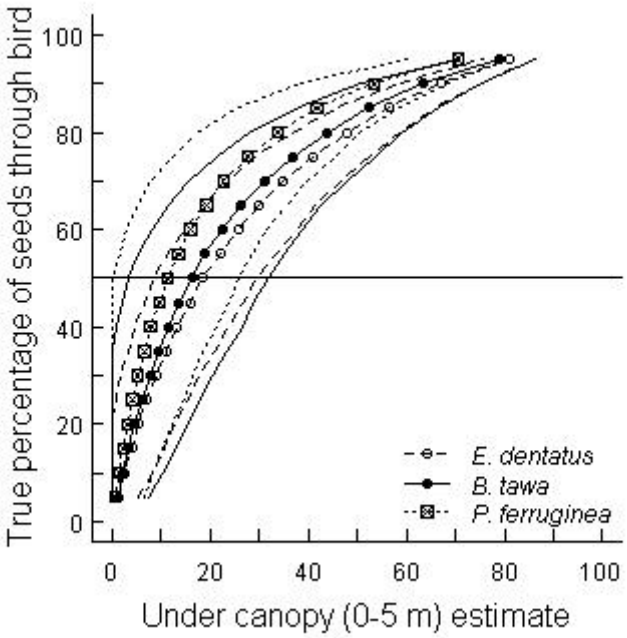

Figure 4.5 True percentage of seed crop consumed by birds as a function of the estimated percentage of crop consumed near the tree (estimate from 0-5 m band) for three species; *Beilschmiedia tawa*, *Elaeocarpus dentatus*, and *Prumnopitys ferruginea*. Corresponding solid and dashed lines without points show 95% credible intervals.

Discussion

Despite the importance of understanding seed dispersal patterns, field studies designed to examine seed shadows have been relatively rare (Hoppes 1988; Kitajima & Augspurger 1989; Laman 1996; Clark *et al.* 1999). Such studies are generally conducted to obtain the seed shadow pattern of clean seeds (in order to determine where animals place seeds) and fleshed seeds are typically not mentioned. New Zealand is a good place to explore the relationship between distance and dispersal quantity due to the lack of native ground-dwelling mammals and rarity of introduced mammals that remove and cache fallen seeds and fruit. This transect approach is novel in allowing cleaned and fleshed dispersal kernels to be estimated. From this, I determined the percentage of seeds that had been through a bird at increasing distance from the parent tree.

However, some assumptions of this system should be considered for possible effects on the conclusions. Firstly, I have no information on whether the nearest tree is the parent of the seeds found. However, because I am interested in estimating total dispersal quantity (a calculation that makes no assumptions about parentage), all I need to know is how distance affects the percentage

of seeds that have been through a bird. Secondly, searching was carried out away from fruiting trees on the edge of a conspecific patch, moving out into forest dominated by other tree species. I then multiplied up to estimate the total fruit crop by extrapolating the linear transect into a full circle, effectively assuming the transect data could be applied to a single isolated tree. Whether this assumption might skew the estimates is unknown. Thirdly, searching was carried out only to 50 m from the parent. Clearly some seeds will be dispersed further than this, but estimation becomes increasingly difficult because the density of seeds becomes very low, yet the area becomes very large. In principle, one would expect that increasing the search radius out to the maximum seed dispersal distance (probably >1 km) would further increase the estimated percentage through a bird. However, the relatively flat slopes found in this study for overall percent clean as search radius increased from 30 to 50 m suggest that this effect might be modest. Therefore, the study methods used were not perfect, but the methodological biases are unlikely to qualitatively change the overall conclusions.

I found that dispersal quantity below the parent tree is a serious underestimate of total dispersal quantity, across the whole range of true dispersal values. In broad terms, high values for dispersal quantity under the canopy (e.g. approximately 80%) indicate very high values for the whole seed crop (approximately 95%); middling values under the canopy indicate high values overall (e.g. 50% indicates 80%); and low values under the canopy indicate middling values overall (e.g. 15% indicates 50%). Therefore, a high percentage consumed under the canopy indicates good dispersal, but even a low percentage consumed under the canopy can indicate that a majority of the whole seed crop is consumed. This has implications for interpreting dispersal quantity in other species. The degree of underestimation I found can be used to estimate total dispersal quantity when sampling has only been conducted below the parent tree, which should be a useful tool for conservation managers. The data collected for *B. tawa* over eight years produced curves similar to those of *E. dentatus* and *P. ferruginea*, which were collected in only one season. This gives confidence that similar data may easily be obtained for other tree species, even over short time frames.

An important benefit from having a high dispersal quantity is escape from pests and pathogens (Janzen 1970; Connell 1971). Seed dispersal by birds can allow plants to reach habitats away from the parent plant that are more favourable for survival, which might not be possible through abiotic vectors alone. Janzen-Connell effects are generally believed to be important in tropical forests (Wright 2002). A meta-analysis by Hyatt *et al.* (2003) claimed no general support for Janzen-Connell effects, however, in their analysis most studies were of short-term removal of seeds from caches on the ground, while longer term studies, which were acknowledged to be more likely to show an effect, had few cases. Two studies have found evidence for Janzen-Connell effects in New Zealand

plant species including *B. tawa*, *Dacrycarpus dacrydioides* (Jana 2012), *Beilschmiedia tarairi* and *Corynocarpus laevigatus* (Wotton & Kelly 2011). Because seed and seedling survival is often higher away from the parent plant (Janzen 1970; Connell 1971; Augspurger 1983; Howe *et al.* 1985), one measure of the relative effectiveness of dispersal is the percentage of the seed crop that is dispersed away from the canopy. I found that 60-78% of all seeds were dispersed beyond 10 m.

Models based on movements and gut retention times are more suited to studying long-distance dispersal events. One such study found that kereru dispersed *B. tawa* seeds on average 95 m away from the parent plant (Wotton & Kelly 2012). Another study on kereru feeding on *P. ferruginea* fruit revealed that 35% of ingested seeds were defecated beneath the parent tree, 40% were deposited 10-30 m away and a few (<2%) were transported over 1 km from their source (Clout & Tilley 1992). However, kereru are not the sole dispersers, and smaller birds that fly shorter distances will typically have shorter dispersal distances and shorter gut passage times (O'Connor 2006; Wotton & Kelly 2012). Tui have been recorded feeding on *B. tawa* (Booth 1984), while tui, bellbirds and blackbirds also feed on *P. ferruginea* (O'Donnell & Dilks 1994; Kelly *et al.* 2010).

The quantity of seeds dispersed is an important aspect of seed dispersal, since it gives an indication of how well the interaction is faring in the presence of bird declines, which have been proposed to put dispersal at risk (Corlett 2007). In New Zealand, it has been argued that dispersal mutualisms were threatened by the extinction or decline of several large bird frugivores (including kereru), reducing the number of effective dispersers, especially for plants with large fruits (> 10 mm diameter) (Clout & Hay 1989). It was claimed that for these plants, kereru were now virtually the sole dispersers. However, a recent review found that dispersal risk may have been over-emphasised, with little empirical evidence for actual dispersal failure (Kelly *et al.* 2010). This study of dispersal quantity supports that view. Presenting earlier data for *B. tawa* at Blue Duck Reserve, Kelly *et al.* (2010) suggested that an average dispersal quantity of 50% below the canopy represents reasonably good dispersal service. We now know that this represents an average of 85% of the seed crop was removed, and so this is definitely good dispersal service. *Prumnopitys ferruginea* is known to be a favoured food of kereru and a high dispersal quantity has been previously found. An individual kereru was estimated to have taken 85% of the total crop (c. 10 000 fruits) from a single *P. ferruginea* tree in a 4 month fruiting season (Clout & Hay 1989). These high dispersal quantities are especially encouraging given that the plant species are among the largest-seeded in the New Zealand flora, and potentially more at risk of being dispersal-limited because fewer frugivorous birds are large enough to disperse seeds. However, they also highlight the importance of individual kereru, since for every bird lost, a vast number of seeds may not be dispersed.

Dispersal service may not be this high in other areas or for other plant species. Kelly *et al.* (2010) reviewed studies of dispersal service to New Zealand plants and found a range from good dispersal service, to one case that showed very poor dispersal (Anderson *et al.* 2006). Clearly, local bird densities can have an important influence on dispersal quantity at a site. Also, if plants have strongly varying seed crop size among years (mast seeding), the size of the seed crop will also be important.

In this study, I quantified the relationship between dispersal quantity below the parent canopy and total dispersal quantity. Dispersal quantity below the parent tree was far more biased towards low dispersal quantity than expected, but my results allow the effect of that bias to be estimated. With observed dispersal quantities of 81-91%, I found that *B. tawa, E. dentatus* and *P. ferruginea* were all receiving good dispersal service, at least at the sites tested here. This is good news in light of bird declines in New Zealand, and is consistent with the conclusion by Kelly *et al.* (2010) that dispersal mutualisms in New Zealand appear to still be functioning adequately. Whether a similar pattern occurs worldwide will require further study. Further plant species also require examination, and I hope that these results add to the toolbox of methods for conservation workers. However, data for three species suggest that only the most extreme evidence for low dispersal quantity underneath the canopy actually indicates dispersal failure at the level of the entire seed crop.

Appendix 4.1 WinBUGS code for 2Dt dispersal modelling of *B. tawa*

```
# MODEL 1: all free
model;
{
# likelihood (poisson)
# count has a poisson distribution with a mean mu
for(t in 1:2){
for(y in 1:8){
for(d in 1:50){
count[y,t,d] ~ dpois(mu[y,t,d])
}}}
# 2Dt:
# the mean of the poisson distribution depends on year, distance and type of seed
# here, beta, u and p - all depend on yr and seed type
for(t in 1:2){
for(y in 1:8){
for(d in 1:50){
mu[y,t,d] <- beta[t,y]*n[y]*p[t,y]/3.1415926/u[t,y]/pow(1+pow(d,2)/u[t,y],p[t,y]+1)
}}}
# prior distributions for all beta, p, u
# in this model, each of those is an array of 2 types * 8 years
for(t in 1:2){
for(y in 1:8){
beta[t,y] ~ dunif(0,1.0E+7)
p[t,y] ~ dunif(.5,10)
u[t,y] ~ dunif(0,1.0E+7)
}}
# monitoring
# seed- distance- specific average estimate
for(t in 1:2){
for(d in 1:50){
for(y in 1:8){
mu.term[y,t,d] <- mu[y,t,d]/n[y]
}
```

```
mu.ave[t,d] <- mean(mu.term[1:8,t,d])
}}
# MRSE
for(t in 1:2){
for(y in 1:8){
for(d in 1:50){
res2[d,t,y] <- pow(count[y,t,d]-mu[y,t,d],2)
}}}
mrse <- mean(res2[,,])
# proportion
# the proportion must be weighed by area to take into account increasing circles
for(y in 1:8){
for(d in 1:50){
# estimated number of seeds in round d (multiplied by the area)
for(t in 1:2){
mu.area[y,t,d] <- mu.term[y,t,d]*3.1415926*(2*d-1)
}
prop[y,d] <- sum(mu.area[y,2,1:d])/(sum(mu.area[y,1,1:d])+sum(mu.area[y,2,1:d]))
}}
for(y in 1:8){
prop.tot[y] <- sum(mu[y,2,1:50])/(sum(mu[y,1,1:50])+sum(mu[y,2,1:50]))
}
# MRSE for props
for(y in 1:8){
res2.prop[y] <- pow(prop.tot[y]-prop.est[y],2)
}
mrse.prop <- mean(res2.prop[])
} # model ends
# INITIAL VALUES
list(
beta=structure(.Data=c(10000,10000,10000,10000,10000,10000,10000,10000,10000,10000,10000,
10000,10000,10000,10000,10000),.Dim=c(2,8)),
p=structure(.Data=c(1,1,1,1,1,1,1,1,1,1,1,1,1,1,1,1),.Dim=c(2,8)),
u=structure(.Data=c(200,200,200,200,200,200,200,200,200,200,200,200,200,200,200,200),
.Dim=c(2,8)))
```

Appendix 4.2 R code for modelling variable true proportions of bird-dispersed seeds on the proportion of bird-dispersed seeds at a given search radius

```
# simulating proportions from the coda-estimates for mu
mu.coda <- read.table('muave_coda_values.txt')[,2]
mu.coda <- array(mu.coda,dim=c(5000,100))
mu.f <- t(mu.coda[, 1:50 ])
mu.c <- t(mu.coda[,51:100])
rm(mu.coda)
# the above is not area adjusted
# sum total with adjustment for area
ring.area <- pi*(2*(1:50)-1)
mu.f.tot <- ring.area%*%mu.f
mu.c.tot <- ring.area%*%mu.c
# we want mu.c.tot=p*(mu.c.tot+mu.f.tot)
# i.e. mu.c.tot = p/(1-p)*mu.f.tot
p.val <- seq(.05,.95,.05) # different true proportion clean
d.val <- seq(5,50,5) # distance
p.lo <- p.md <- p.mn <- p.hi <- array(dim=c(length(p.val),length(d.val)))
for(i in 1:length(p.val)){
p <- p.val[i];print(p)
mu.coef <- p/(1-p)*mu.f.tot/mu.c.tot
mu.f.sim <- mu.f
mu.c.sim <- t(t(mu.c)*c(mu.coef))
# check
mu.f.tot.sim <- ring.area%*%mu.f.sim
mu.c.tot.sim <- ring.area%*%mu.c.sim
# should be constant
table(mu.c.tot.sim/(mu.c.tot.sim+mu.f.tot.sim))
y.c <- array(rpois(5000*50,mu.c.sim),dim=dim(mu.c.sim))
y.f <- array(rpois(5000*50,mu.f.sim),dim=dim(mu.f.sim))
for(dd in 1:length(d.val)){
# posterior simulations
```

```
y.tot.c <- ring.area[1:d.val[dd]]%*%y.c[1:d.val[dd],]
y.tot.f <- ring.area[1:d.val[dd]]%*%y.f[1:d.val[dd],]
p.est <- y.tot.c/(y.tot.f+y.tot.c)
p.lo[i,dd] <- quantile(p.est,.025)
p.hi[i,dd] <- quantile(p.est,.975)
p.md[i,dd] <- quantile(p.est,.5)
p.mn[i,dd] <- mean(p.est)
}}
```

Chapter 5: Effect of non-dispersal

***Ripogonum scandens* (supplejack) seedlings at high density. Photo: T. Wyman.**

Abstract

Declines of frugivorous animals such as birds, combined with the introduction of mammalian herbivores have prompted concern for recruitment of fleshy-fruited plant populations in many Pacific Islands. Non-dispersal results in whole fruits dropped in high densities below parent trees that may be more vulnerable to seed or seedling mortality due to accumulation of host-specific pathogens or seed predators (Janzen-Connell effects). Janzen-Connell effects were previously thought to be important in tropical forests but not in the temperate zone. However, recent studies have unexpectedly found Janzen-Connell effects operating in temperate forests, and it is important to determine how widespread these effects are by testing further plant species. I investigated the consequences of dispersal failure and the role of introduced mammals in the regeneration of three New Zealand plant species of varying growth forms and seed size; *Elaeocarpus hookerianus*, *Ripogonum scandens*, and *Coprosma robusta*. I compared seed predation, germination, and seedling survival for dispersed and undispersed seeds for up to 21 months in the field in a full factorial design. I compared the fate of seeds under conspecific adults versus 16 m away from the parent, whole fruits versus hand-cleaned seeds, seeds at high versus low densities, and seeds enclosed in mammal-proof cages versus uncaged seeds. Recruitment in all plant species was affected by both dispersal failure and introduced mammalian seed and seedling predators. Mammal exclusion had the greatest effect on survival through decreasing the seed predation of *E. hookerianus* and *R. scandens*, increasing the germination of *C. robusta*, and increasing the seedling survival of *R. scandens* and *C. robusta*. Fruit pulp removal was the most beneficial feature of dispersal, through decreasing seed predation of *R. scandens* and increasing germination of *R. scandens* and *C. robusta* (although this may be a short-term effect). There was little evidence for density- or distance-dependent decreases in survival (Janzen-Connell effects), apart from an increase in germination of *C. robusta* seeds at low density. The combined effects of dispersal failure (under parent, high density, whole fruit) and introduced mammals decreased the number of live seedlings at 21 months by 92% for *E. hookerianus* and 75% for *R. scandens*, and decreased the number of live *C. robusta* seedlings at 10 months by 91%. This study demonstrates the negative effects that introduced mammalian herbivores have on plant recruitment, and the importance of maintaining bird-plant seed dispersal mutualisms as they provide some escape from seed and seedling predation.

Introduction

Worldwide declines of frugivorous birds and mammals threaten to disrupt seed dispersal mutualisms (Sekercioglu *et al.* 2004; Corlett 2007). Animal seed dispersers provide many ecosystem services such as removal of seeds, escape from seed predators, enhanced germination, increased gene flow, and restoration of disturbed ecosystems (Sekercioglu *et al.* 2004). It has been suggested that passage of seeds through a disperser's gut is required for seed germination (e.g. Temple 1977). However, experimental evidence demonstrating this strict germination requirement is generally lacking (Robertson *et al.* 2006; Traveset *et al.* 2007; Kelly *et al.* 2010). Perhaps more important is the transport of seed away from the parent plant. The escape hypothesis, first proposed by Janzen (1970) and Connell (1971), predicts higher mortality of juvenile plants close to parent plants. This is because the high seed and seedling density around parent plants enhances the activity of host-specific seed predators, herbivores, and pathogens, as well as intraspecific competition during the process of seedling establishment. Consequently, seed and seedling survival is predicted to be higher away from parent plants, and it is thought that evolution has favoured the development of seed dispersal mechanisms in order to "escape" this locally high seed mortality (Stoner & Henry 2008).

Janzen-Connell effects are thought to maintain the high plant diversity of tropical forests because the lowered recruitment probability near conspecific adults creates space and allows many other plant species to establish in those sites (Clark & Clark 1984). This explains why most adults of a given lowland tropical tree species appear to be more regularly distributed than if the probability of a new adult appearing at a point in the forest were proportional to the number of seeds arriving at that point (Janzen 1970). Janzen-Connell effects were thought to be important in tropical ecosystems, but not temperate ones due to higher abundances of natural enemies and a greater degree of natural enemy specialisation in aseasonal tropical habitats (Janzen 1970). Janzen and Connell theorized that the unpredictable fluctuations in the physical environment of temperate forests (such as weather changes) may cause fluctuations in seed or seedling predators, lifting the predation pressure from juvenile plants. As a result, few studies of Janzen-Connell effects have been conducted in temperate forests, compared to very many studies in tropical forest systems. There is however, an increasing number of studies showing that Janzen-Connell effects are in fact also important in temperate plant species (Packer & Clay 2000; Wotton & Kelly 2011). HilleRisLambers *et al.* (2002) found that the proportion of temperate species affected by density-dependent mortality is equivalent to that in tropical forests. According to Wenny *et al.* (2011), one of the key remaining questions concerning seed dispersal is how widespread density- and distance-dependent seed and

seedling mortality effects are, both in the tropics and in the temperate zone, because these greatly increase dependence on dispersers.

According to Schupp *et al.* (2002), dispersal limitation can occur when few seeds are dispersed, many seeds are dispersed short distances, or seeds are dispersed patchily so that some sites receive high seed numbers and others receive few. While both density- and distance-dependent enemies are important, most studies of Janzen-Connell effects fail to distinguish between them. For animal-dispersed plants, high densities of seeds can occur away from the plant as well as under, due to the behaviour of the dispersing animal. For example, high densities of seeds are often found beneath bird perches (spatially contagious seed dispersal; Schupp *et al.* 2002). If density-dependent mortality acts on seed clumps away from conspecific adults, spatially contagious seed dispersal could limit recruitment in a similar fashion to a lack of dispersal altogether (Schupp *et al.* 2002).

As is the case for other island archipelagos of the Pacific, New Zealand has suffered from the recent arrival of humans and the introduction of mammalian predators that caused native vertebrate extinctions and declines. Today, 41% of endemic forest bird species present pre-human are now extinct (Innes *et al.* 2010), while others are functionally extinct (sensu Sekercioglu *et al.* 2004) and persist only in small, isolated sanctuaries. Dispersal of native fleshy fruits in New Zealand is now almost entirely dependent on four native birds; silvereyes (*Zosterops lateralis*), bellbirds (*Anthornis melanura*), tui (*Prosthemadera novaeseelandiae*) and kereru (*Hemiphaga novaeseelandiae*) (Kelly *et al.* 2006). Introduced mammals not only reduce native bird numbers through predation of eggs, chicks and adults (Moors 1983; Brown 1993; Clout *et al.* 1995), but may also directly limit plant recruitment. Mammalian herbivores have been shown to prevent seed production (Cowan & Waddington 1990; Cowan 1991; Dijkgraaf 2002), destroy seeds (Beveridge 1964; Daniel 1973; Campbell & Atkinson 2002), and graze on seedlings (Nugent *et al.* 2001; Wilson *et al.* 2003). Consequently, plants in New Zealand may be vulnerable to recruitment failure from the combined effects of dispersal limitation due to reduced frugivorous bird densities, and the negative effects of mammalian seed and seedling predation.

Higher seed or seedling mortality near parent trees due to pathogens or seed predators could greatly increase the ecological and evolutionary importance of bird dispersal, and increase the negative consequences of its failure. Janzen-Connell effects have been found in four New Zealand tree species: *Beilschmiedia tarairi*, *Corynocarpus laevigatus* (Wotton & Kelly 2011), *Beilschmiedia tawa*, and *Dacrycarpus dacrydioides* (Jana 2012). Worldwide, the majority of species studied investigating Janzen-Connell effects are canopy trees, whereas few lianas or shrubs have been considered (Carson *et al.* 2008). Janzen and Connell considered seed size to be an important trait influencing the amount of predation on a seed crop.

In this study I investigated the consequences of dispersal failure for regeneration of three widespread New Zealand plant species; *Elaeocarpus hookerianus*, *Coprosma robusta*, and *Ripogonum scandens*. I also investigated the role of introduced mammals in limiting the recruitment of these plant species. I used a manipulative factorial experiment to examine whether post-dispersal seed predation, germination, or seedling survival were affected by: (1) movement of seeds away from adult conspecifics; (2) seed density; (3) fruit pulp removal; and (4) exclusion of introduced mammals. I predicted that Janzen-Connell effects would be evident in the tree, *E. hookerianus*, but less so in the small-seeded successional shrub, *C. robusta*. Although the vine, *R. scandens*, has large seeds, due to its growth habit of forming thick, intertwining masses of plants, I predicted that Janzen-Connell effects would be less evident in this species also.

Methods

Study species

The three study species varied in life form and seed size (Table 5.1). *Elaeocarpus hookerianus* Raoul (pokaka, Elaeocarpaceae) is one of three endemic species in this family in New Zealand. *Elaeocarpus hookerianus* is an evergreen tree, generally growing to a height of around 16 m. It is common in lowland to montane forests throughout much of the North and South Islands, but uncommon north of Auckland (Poole & Adams 1994). *Elaeocarpus hookerianus* has a distinct juvenile form where its branches are interlaced and have very small leaves. The fruit are purplish single-seeded drupes and are medium-sized relative to the New Zealand flora.

Ripogonum scandens J.R. et G. Forst. (supplejack, Ripogonaceae) is an endemic species of the sole genus in the family. It is a common woody, evergreen, twining liane occurring throughout New Zealand in coastal to montane forests (Poole & Adams 1994). *Ripogonum scandens* begins life as a sappy stem searching for support, and once it finds a shrub or tree to twine around it grows upwards to access sunlight, where it then develops branches and leaves. *Ripogonum scandens* bears red fleshy fruits throughout the year. The fruits are fairly large (the 10th largest mean diameter of New Zealand species), and can have up to 4 seeds, but most often have only one (Kelly *et al.* 2010).

Coprosma robusta Raoul (karamu, Rubiaceae) is one of approximately 90 *Coprosma* species, with about half of these found in New Zealand (Poole & Adams 1994). *Coprosma robusta* is an endemic species found in lowland forest or scrub throughout New Zealand (Poole & Adams 1994). The plant is a very widespread and successful, fast growing, early successional shrub/small tree that grows up to 6 m tall, with small orange drupes that nearly always contain 2 seeds.

Table 5.1 Characteristics of the plant species studied. Counts and measurements were done on random samples of 15 freshly collected fruit and thoroughly air-dried seeds. Values are means ± standard errors.

Species	Family	Plant type	Seeds per fruit	Fruit size (mm)		Seed size (mm)	
				Length	Diameter	Length	Diameter
E. hookerianus	Elaeocarpaceae	Tree (15 m)	1	11.2 ± 0.2	6.5 ± 0.1	9.8 ± 0.1	5.1 ± 0.1
R. scandens	Ripogonaceae	Liana	1.2 ± 0.1	11.8 ± 0.3	10.0 ± 0.2	7.2 ± 0.2	6.5 ± 0.2
C. robusta	Rubiaceae	Shrub (6 m)	2	6.6 ± 0.2	4.3 ± 0.1	3.5 ± 0.1	1.8 ± 0.1

Study sites

This study was carried out at two sites in Canterbury, South Island, New Zealand (Fig 5.1). Germination experiments for *Elaeocarpus hookerianus* were carried out at Lords Bush Scenic Reserve. Lords Bush (43°29'S, 171°93'E, 400 m elevation) is a 12 ha remnant of lowland beech/podocarp hardwood forest on the Canterbury Plains. It is located at the base of the Torlesse Range, north of Springfield. *Dacrycarpus dacrydioides* (kahikatea), *E. hookerianus*, and *Nothofagus solandri* (black beech) dominate the forest canopy, over a subcanopy of mainly *Griselinia littoralis* (broadleaf) and *Carpodetus serratus* (putaputaweta) (Williams & Buxton 1986). There are also *Prumnopitys taxifolia* (matai), *Coprosma* species, *Pseudowintera colorata* (horopito), *Myrsine divaricata* (weeping matipo), and *Rubus* species present (Williams 2005). Sheep and cattle have grazed in the bush in the past, but it is now partially fenced and a dense scrub of *Ulex europaeus* (gorse) and *Rubus fruticosus* (blackberry) has developed on the margins, limiting ungulate access (Williams & Buxton 1986).

Germination experiments for *Ripogonum scandens* and *Coprosma robusta* were conducted at Hay Scenic Reserve. Hay Reserve (43°70'S, 172°90'E, 35 m elevation) is a 6 ha forest remnant in Pigeon Bay, Banks Peninsula. The forest canopy consists mainly of large *D. dacrydioides*, *P. taxifolia*, *Podocarpus totara* (totara) and *Prumnopitys ferruginea* (miro). There are also *Alectryon excelsus* (titoki), *Elaeocarpus dentatus* (hinau), *E. hookerianus*, *Macropiper excelsum* (kawakawa), *Melicytus ramiflorus* (mahoe), *Pittosporum eugenioides* (lemonwood) and *Hedecarya arborea* (pigeonwood). Planted *Populus* and other exotics occur around the edges of the podocarp-hardwood forest, although some of these have been removed in recent years.

Introduced mammals such as rodents (*Rattus rattus*, *Mus musculus*) and brushtail possums (*Trichosurus vulpecula*) are present at both sites. There is some trapping of mustelids (e.g. ferrets (*Mustela furo*) and stoats (*M. erminea*)) and possums, and these animals invade from surrounding farmland. At both sites frugivorous birds present include native kereru, silvereye and bellbird, and

introduced song thrush (*Turdus philomelos*), blackbird (*Turdus merula*) and starling (*Sturnus vulgaris*). Tui are absent at both sites.

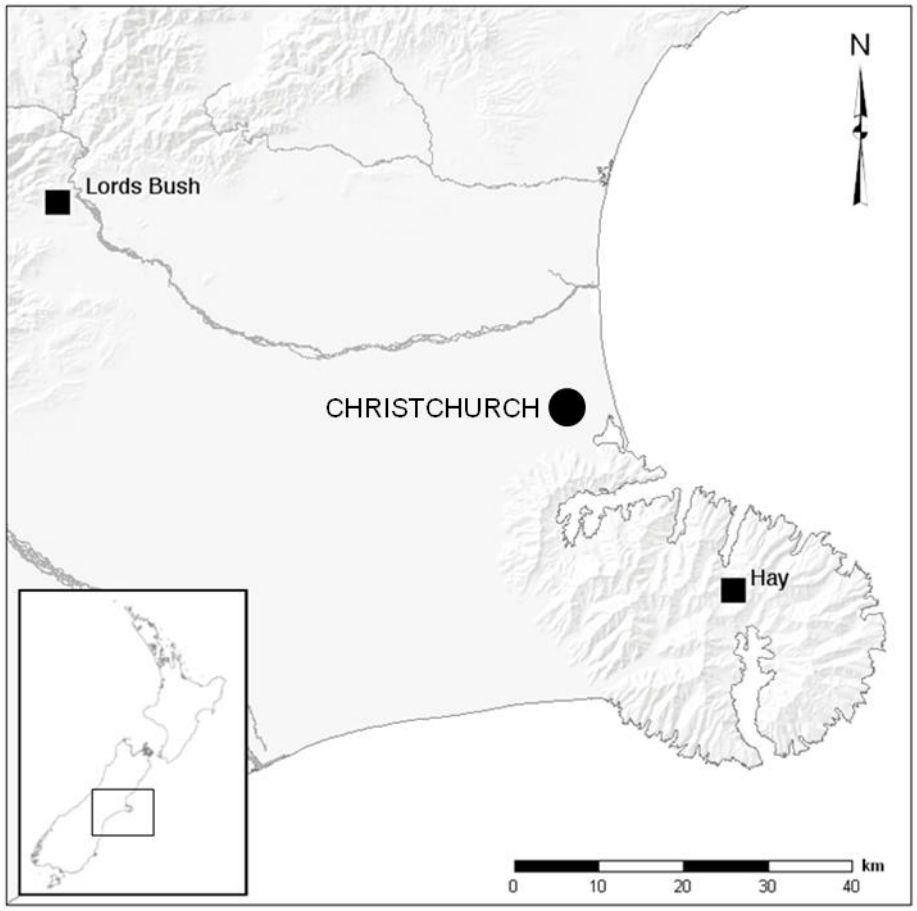

Figure 5.1 Location of study sites relative to Christchurch in the South Island, New Zealand.

Experimental design

I conducted a field experiment to compare the fate of dispersed and undispersed seeds of *E. hookerianus, R. scandens* and *C. robusta*, following the methods of Wotton and Kelly (2011). I used a split-plot full-factorial design with four treatments, each with two levels: (1) under a fruiting conspecific adult (referred to as a parent) versus 16 m away from the nearest conspecific; (2) whole fruits versus seeds with the pulp removed (by hand); (3) high versus low seed density (40 or 10 seeds/fruits, respectively); and (4) mammal exclusion versus open access. Each parent plant was paired spatially with a location 16 m away. Fruit, density, and exclusion treatments were grouped in subplots under and away from parents (the plot level of replication). I used a distance of 16 m for 'away' plots as I was unable to obtain sufficient replicates using greater distances without coming near another conspecific tree.

For each species, ripe fruits were collected from or beneath at least five different individual fruiting plants and combined prior to randomly allocating them to treatments. The pulp was removed from seeds by hand-cleaning (rather than via passage through a bird). Previous studies have found that compared with the deinhibition effect of cleaned seeds versus whole fruit, the scarification effect of hand-cleaning seeds versus passage through a bird is relatively small for most species (Robertson *et al.* 2006; Kelly *et al.* 2010).

To prevent seeds from rolling away, they were placed within 7 cm wide strips of lexan polycarbonate (1 mm thick) with the ends stapled together to construct 10 cm diameter tubes open at the top and bottom (Fig 5.2a). Tubes were inserted into the soil approximately 1 m apart, with around 5 cm of the tube remaining above ground, and fixed to the ground using two metal pegs. To exclude vertebrate seed and seedling predators I constructed cages made of welded galvanized mesh with 5 mm aperture, 20 cm diameter and 30 cm high (Fig 5.2b). The mesh size was small enough to exclude all mammals present, including house mice (*Mus musculus*). These cages were placed over the tubes and secured to the ground with metal pegs. I randomly assigned the eight treatment combinations to tubes in the subplot.

This design was replicated at six parent plants at Lords Bush for *E. hookerianus*, and at Hay for both *R. scandens* and *C. robusta*. *Elaeocarpus hookerianus* and *R. scandens* plots were set up in July 2011, and monitored for 21 months. These plots were monitored every 2 months for the first 4 months, and every 6 months thereafter. *Coprosma robusta* plots were set up in July 2012, and monitored at 2, 8, and 10 months. At each visit, I recorded insect and mammal predation (for *E. hookerianus* and *R. scandens* only), seedling emergence, and seedling survival. Seed disappearance and predation was monitored for *E. hookerianus* and *R. scandens*, but was not possible for *C. robusta* due to the small seed size. Insect-eaten seeds were characterised by small holes in the seed or seed coat. Mammal-eaten seeds generally had 2-3 mm wide tooth marks and/or holes consistent with rodent predation (Beveridge 1964). No seeds that were partially eaten by insects or mammals germinated. For the purpose of this analysis I assumed seeds that disappeared were killed, as I found no evidence of seed caching, congruent with Wilson *et al.* (2007). Seed germination was classified as the appearance of cotyledons above-ground. Seedling height was recorded as either less than or taller than 5 cm, to help distinguish between newly emerged seedlings and those that had emerged earlier. At each visit, I placed a small amount of litter inside the tubes to reduce the effect of interception of litter-fall by cages.

To compare germination of seeds in the field to that in a controlled environment, hand-cleaned seeds of each species were sown in trays of potting mix and placed in an unheated glasshouse, concurrently to when the field experiments were set up. Between 200 and 700 seeds of each species

were planted, with 30-50 in a tray each, and germination recorded every 2-3 months for 21 months (*E. hookerianus* and *R. scandens*) or 10 months (*C. robusta*).

a)

b)

Figure 5.2 a) Whole *E. hookerianus* fruits at high density in a 10 cm diameter experimental tube. b) Mammal-proof cage covering an experimental tube with *R. scandens* seedlings.

Data analysis

I used generalised linear mixed models (GLMM) to analyse the effects of distance (near versus away); mammal exclusion (open versus caged); fruit (clean versus whole); and density (high versus low) on total seed predation (including insect predation, mammal predation and removed seeds); seedling emergence (for unpredated seeds); and seedling survival (for germinated seeds). Because seedling emergence for *E. hookerianus* did not occur until the latter part of the monitoring period, survival was not analysed for this species. Since all the *C. robusta* fruits that were measured had two seeds per fruit, I multiplied the number of whole fruits sown by two to correct for this before analysing the data.

GLMMs allow the use of non-normal error distribution and hierarchical random effects. I used a binomial error distribution with associated logit link for all models, with number of successes and number of failures as the response variable. I included plots nested within parent trees as random effects in all models. When data were overdispersed I included an observation-level random effects parameter (Bates *et al.* 2013). I chose *a priori* to include all single factors in the models (distance, density, fruit, exclosure). Since predation could be distance, density, or fruit-type responsive, I included the exclosure:distance, exclosure:density, and exclosure:fruit interactions in a second set of models, and in each case compared the simple model with no interactions with the model including interactions using ANOVA. The simpler model was used unless the model including interactions was significantly better ($p < 0.05$). For all the analyses I used the "lmer" function included in the lme4 package (Bates *et al.* 2013) in the statistical program R, version 2.15.1.

Results

Seed predation

Over all seeds (both clean and whole), predation occurred on 40.6% of *E. hookerianus* seeds and 9.1% of *R. scandens* seeds. Seed predation was of three types: seeds disappeared from the tubes and were presumed to have been removed by mammals; chew marks and/or holes consistent with mammalian predation (Fig 5.3); and small holes in the seed coat consistent with insect predation. Of these three types of predation, most was removal of whole fruits by mammals (Table 5.2). Mammalian seed predation only occurred when tubes were not protected by cages, and insect seed predation (that was visible) was rare (Table 5.2).

Table 5.2 Total number of predated *E. hookerianus* and *R. scandens* seeds, and percentages of the three types of seed predation (removed, mammal, or insect). Numbers within brackets indicate the percentage of each predation type that occurred on whole fruits, as opposed to clean seeds (i.e. 50% would indicate no preference).

Species	n predated seeds (% of total seeds)	Percentage of seed predation types			
		Removed	Mammal	Insect	Total
E. hookerianus	975 (40.6)	95.7 (58.1)	2.5 (45.8)	1.8 (33.3)	100
R. scandens	219 (9.1)	98.6 (57.9)	0	1.4 (33.3)	100

Figure 5.3 *Elaeocarpus hookerianus* seed predation, probably by ship rats.

The seed predation model that included exclosure interactions was significantly better than the model with no interactions for *E. hookerianus* ($\chi^2_{(3)} = 14.973$, $p = 0.002$), but not for *R. scandens* ($\chi^2_{(3)} = 5.844$, $p = 0.120$). Predation on seeds with open access to mammals was significantly higher than on caged seeds (Table 5.3). *Elaeocarpus hookerianus* seed predation in the open was on average 79.5%, compared to 1.3% in cages, while *R. scandens* seed predation in the open was 17.1%, compared to 0.2% in cages (Fig 5.4). For both species, whole fruits incurred higher predation than clean seeds (Fig 5.4). The effect of pulp removal decreasing seed predation was statistically significant for *R. scandens*, and was dependent on exclosure for *E. hookerianus*, with whole fruits incurring higher predation than clean seeds in the open, but not when caged (Table 5.3).

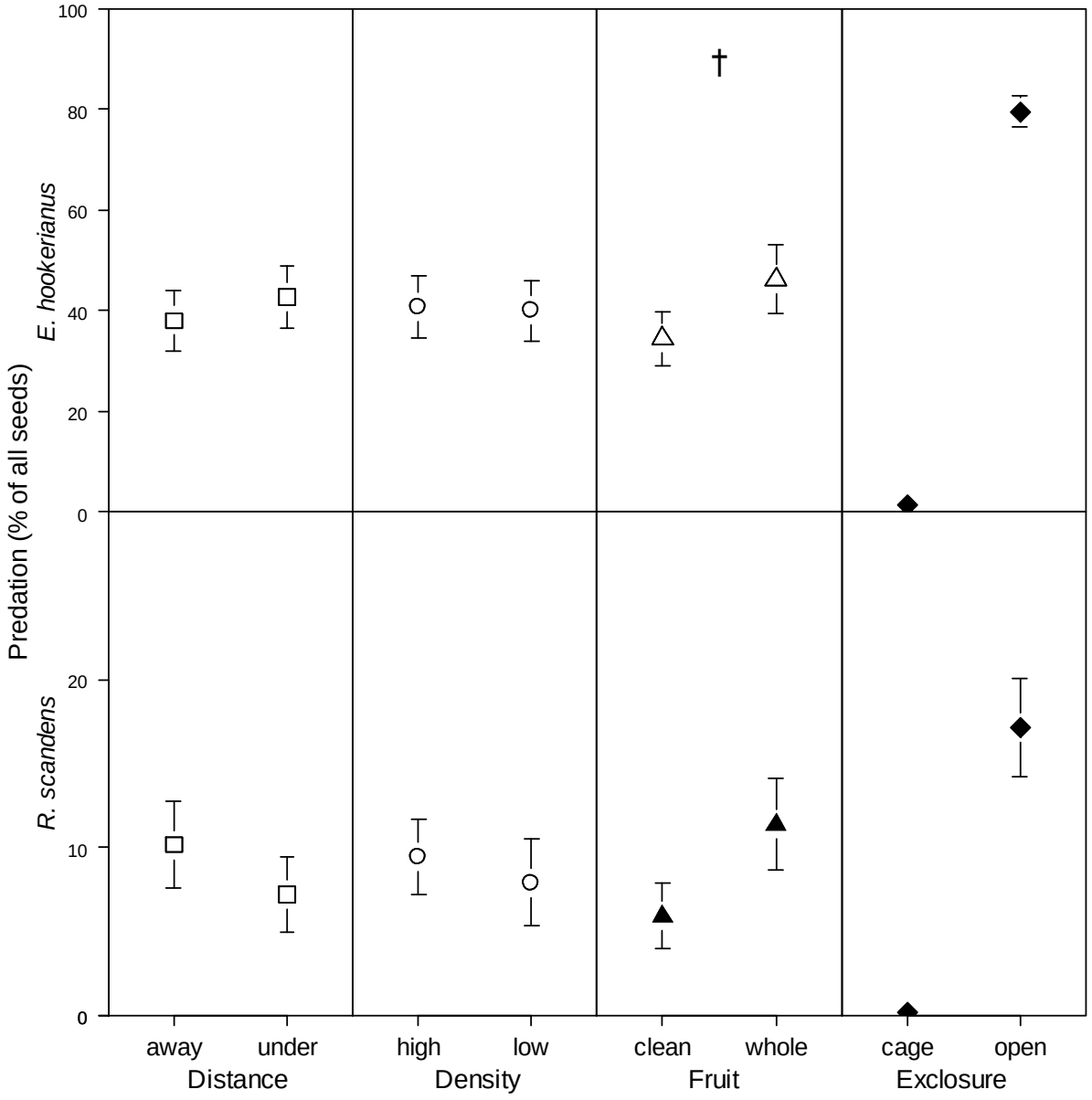

Figure 5.4 Main treatment effects on mean percentage of predated seeds (± SE) for *E. hookerianus* and *R. scandens.* Note means are raw values. Filled symbols represent significant treatment effects ($p < 0.05$) obtained from GLMMs, † = significant through interaction with exclosure (see Table 5.3).

Table 5.3 Binomial GLMM parameter estimates for main treatment effects on percentage of predated *E. hookerianus* and *R. scandens* seeds.

Species	Parameter	Estimate	Std. error	z value	p value
E. hookerianus	Intercept	-5.679	0.830	-6.840	<0.001
	DistanceUnder	-0.052	0.811	-0.064	0.949
	FruitWhole	-0.472	0.818	-0.576	0.564
	ExclosureOpen	6.448	0.808	7.978	<0.001
	DensityLow	1.359	0.811	1.676	0.094
	ExclosureOpen:DistanceUnder	0.681	0.881	0.772	0.440
	ExclosureOpen:DensityLow	-1.697	0.884	-1.920	0.055
	ExclosureOpen:FruitWhole	2.698	0.896	3.011	0.003
R. scandens	Intercept	-8.090	1.417	-5.711	<0.001
	DistanceUnder	-0.412	0.491	-0.839	0.402
	FruitWhole	0.999	0.442	2.260	0.024
	ExclosureOpen	5.843	1.382	4.228	<0.001
	DensityLow	-0.356	0.452	-0.788	0.431

Seedling emergence

Total seedling emergence over the 21 months of monitoring was 3.9% for *E. hookerianus* and 25.1% for *R. scandens*. The first *E. hookerianus* seedlings did not emerge until 14 months after sowing (spring the following year), while the first *R. scandens* seedlings appeared 2 months after sowing (spring the same year). *Coprosma robusta* seedling emergence over 10 months was 9.6% overall, and began 2 months after sowing. For *E. hookerianus*, seedling emergence from clean seeds was 5.9% overall, not significantly different to the emergence of clean seeds sown in the glasshouse of 5.7% ($\chi^2_{(1)} = 0.007$, p = 0.933). For *R. scandens*, seedling emergence from clean seeds was 34.3% overall, not significantly different to the emergence of clean seeds in the glasshouse of 37.6% ($\chi^2_{(1)} = 0.843$, p = 0.359). Germination of clean *C. robusta* seeds was lower in the field (19.7% overall) than in the glasshouse (71.6%) ($\chi^2_{(1)} = 501.649$, p = <0.001).

For all three species, the seedling emergence models including interactions were not significantly better than the models without interactions (*E. hookerianus* $\chi^2_{(3)} = 3.521$, p = 0.318; *R. scandens* $\chi^2_{(3)} = 2.078$, p = 0.556; *C. robusta* $\chi^2_{(3)} = 2.950$, p = 0.399). For all species, seedling emergence was higher for clean seeds than for whole fruits, significantly so for *R. scandens* (mean 37.7% versus 18.2%) and

C. robusta (24.0% versus 5.4%), but not for *E. hookerianus* (10.7% versus 2.5%) (Fig 5.5, Table 5.4). Seedling emergence was significantly higher at low density than high density for *C. robusta* (Fig 5.5, Table 5.4). Excluding mammals also significantly increased observed seedling emergence for *C. robusta* (Table 5.4).

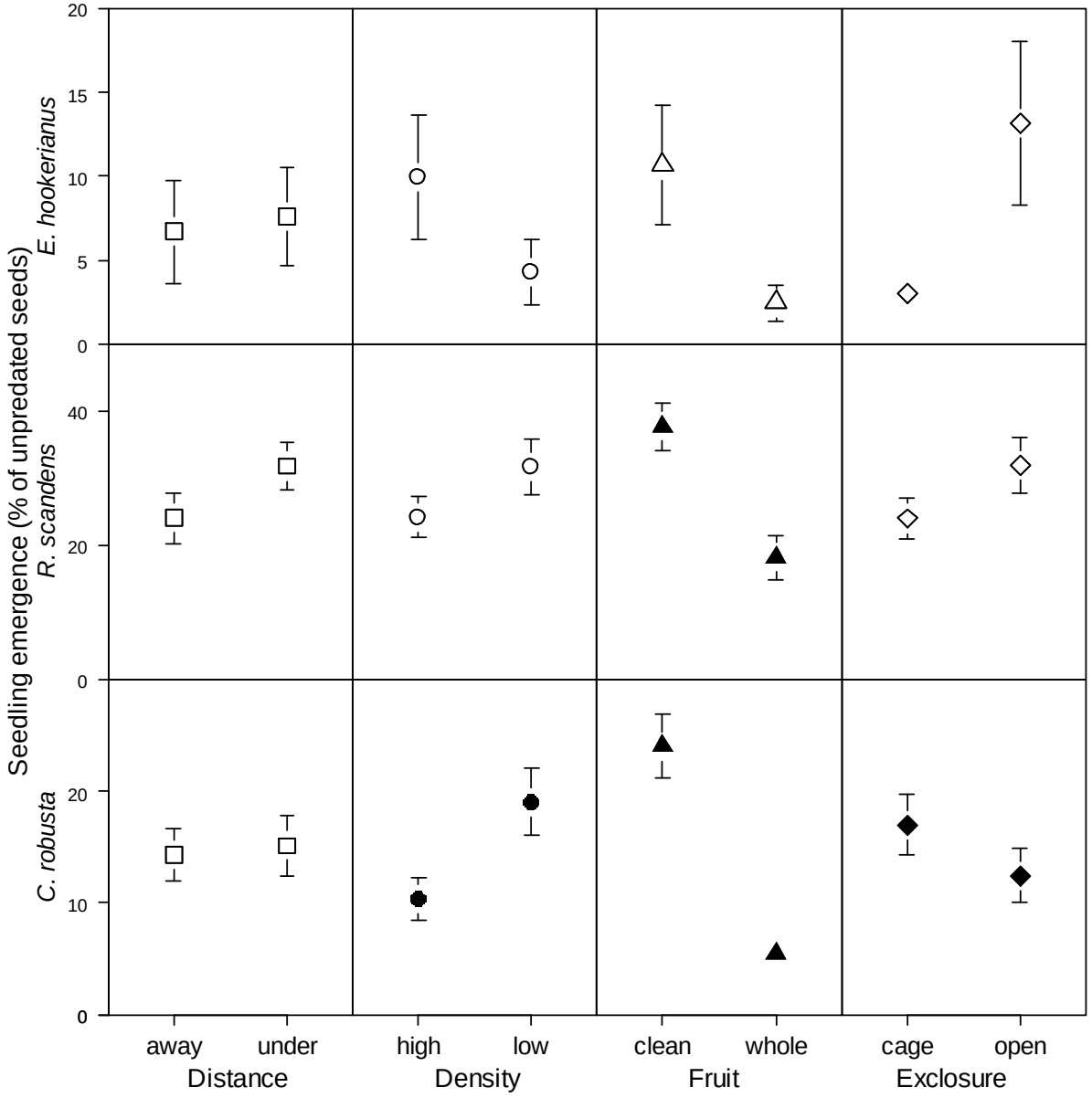

Figure 5.5 Main treatment effects on mean percentage of emerged seedlings (of unpredated seeds, ± SE) for *E. hookerianus*, *R. scandens* and *C. robusta*. Note means are raw values. Filled symbols represent significant treatment effects ($p < 0.05$) obtained from GLMMs (see Table 5.4).

Table 5.4 Binomial GLMM parameter estimates for main treatment effects on percentage of seedling emergence (of unpredated seeds) for *E. hookerianus*, *R. scandens* and *C. robusta*.

Species	Parameter	Estimate	Std. error	z value	p value
E. hookerianus	Intercept	-4.498	0.611	-7.359	<0.001
	DistanceUnder	0.835	0.606	1.377	0.169
	FruitWhole	-1.095	0.671	-1.632	0.103
	ExclosureOpen	1.163	0.636	1.829	0.067
	DensityLow	-0.042	0.632	-0.066	0.947
R. scandens	Intercept	-1.492	0.379	-3.935	<0.001
	DistanceUnder	0.708	0.451	1.571	0.116
	FruitWhole	-1.346	0.249	-5.402	<0.001
	ExclosureOpen	0.414	0.247	1.679	0.093
	DensityLow	0.447	0.250	1.788	0.074
C. robusta	Intercept	-1.640	0.378	-4.341	<0.001
	DistanceUnder	0.001	0.360	0.003	0.997
	FruitWhole	-1.903	0.215	-8.860	<0.001
	ExclosureOpen	-0.627	0.213	-2.942	0.003
	DensityLow	0.916	0.214	4.279	<0.001

Seedling survival

Seedlings of *E. hookerianus* took more than a year to begin emerging, and in total 56 emerged over the monitoring period. Of these, four did not survive to the last count, however, monitoring of seedling survival in this species clearly requires a longer time period, so is not analysed here.

Figure 5.6 Insect herbivory of *R. scandens* seedling.

I observed some insect herbivory of *R. scandens* and *C. robusta* seedlings (Fig 5.6). For both species the seedling survival models including interactions were not significantly better than the models without interactions (*R. scandens* $\chi^2_{(3)} = 1.087$, p = 0.780; *C. robusta* $\chi^2_{(3)} = 2.006$, p = 0.571). Seedlings protected by cages had significantly higher survival than those not caged for both *R. scandens* (55.4% versus 28.2%) and *C. robusta* (42.5% versus 27.9%) (Fig 5.7, Table 5.5). Survival of *C. robusta* seedlings was higher under than away from the parent plant, though marginally non-significant (p=0.092, Fig 5.7, Table 5.5).

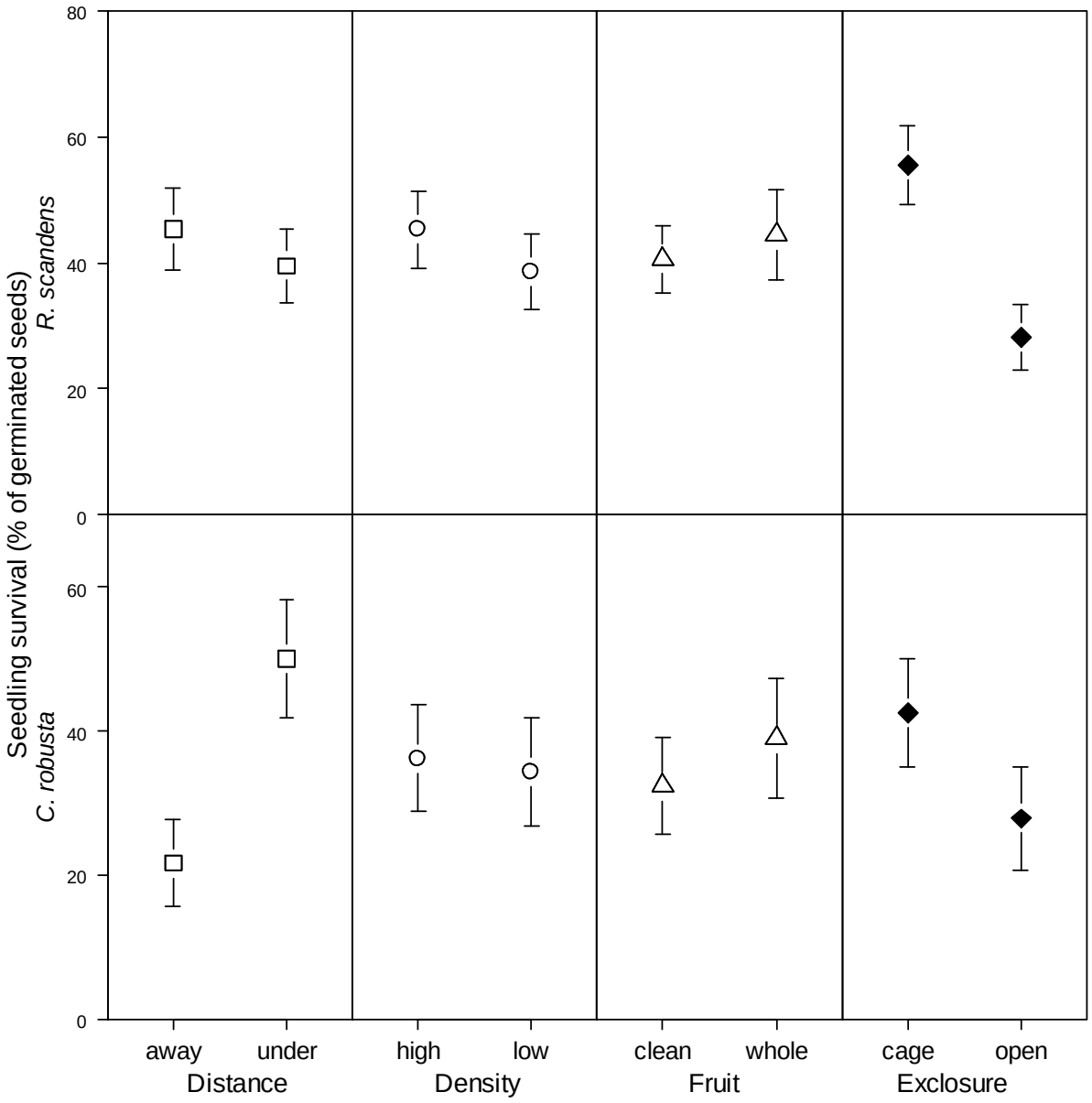

Figure 5.7 Main treatment effects on mean percentage (± SE) of emerged *R. scandens* and *C. robusta* seedlings that survived to the end of the monitoring period (21 months for *R. scandens* and 10 months for *C. robusta*). Note means are raw values. Filled symbols represent significant treatment effects (p < 0.05) obtained from GLMMs (see Table 5.5).

Table 5.5 Binomial GLMM parameter estimates for main treatment effects on percentage of emerged *R. scandens* and *C. robusta* seedlings that survived to the end of the monitoring period (21 months for *R. scandens* and 10 months for *C. robusta*).

Species	Parameter	Estimate	Std. error	z value	p value
R. scandens	Intercept	1.037	0.492	2.108	0.035
	DistanceUnder	-0.378	0.474	-0.798	0.425
	FruitWhole	0.098	0.445	0.221	0.825
	ExclosureOpen	-1.994	0.431	-4.624	<0.001
	DensityLow	-0.593	0.438	-1.352	0.176
C. robusta	Intercept	-6.528	3.572	-1.827	0.068
	DistanceUnder	7.673	4.555	1.685	0.092
	FruitWhole	2.512	2.042	1.230	0.219
	ExclosureOpen	-5.063	2.193	-2.309	0.021
	DensityLow	0.185	1.991	0.093	0.926

Overall effects

Fruit pulp removal decreased seed predation for *R. scandens* and increased germination for *R. scandens* and *C. robusta* (Table 5.6). However, this difference in germination may reflect a delay in germination for whole fruits, rather than a decrease in final germination percentage. Movement of seeds away from the parent plant did not increase survival for any species. Depositing seeds in low density increased the germination of *C. robusta* seeds. Excluding mammals increased the survival of *E. hookerianus* and *R. scandens* seeds at the predation stage, increased the seedling survival of *R. scandens* and *C. robusta*, and increased the germination of *C. robusta* (Table 5.6).

The combined effects of dispersal failure plus introduced mammals decreased the number of live seedlings present at the end of the experiment from 3.8% (away from parent, low density, clean seed, caged) to 0.3% (under parent, high density, whole fruit, uncaged) for *E. hookerianus*, 18.2% to 4.6% for *R. scandens*, and 14.9% to 1.4% for *C. robusta* (Fig 5.8). These are decreases of 92% for *E. hookerianus*, 75% for *R. scandens,* and 91% for *C. robusta*. The decrease in number of live seedlings present at the end of the experiment due to the loss of dispersal alone (under parent, high density, whole fruit, caged) was 70% for *E.* hookerianus, 46% for *R. scandens*, and 73% for *C. robusta* (Fig 5.8).

Table 5.6 Effect of seed dispersal and mammal exclusion treatments on difference in percentage survival of *E. hookerianus*, *R. scandens* and *C. robusta* (calculated from GLMM fitted means). Non-significant effects are indicated by zero.

Recruitment stage	Pulp removal	Away from parent	Low density	Caged
E. hookerianus				
predation	0	0	0	+ 7795
germination	0	0	0	0
R. scandens				
predation	+81	0	0	+37035
germination	+123	0	0	0
survival	0	0	0	+129
C. robusta				
germination	+345	0	+82	+50
survival	0	0	0	+62

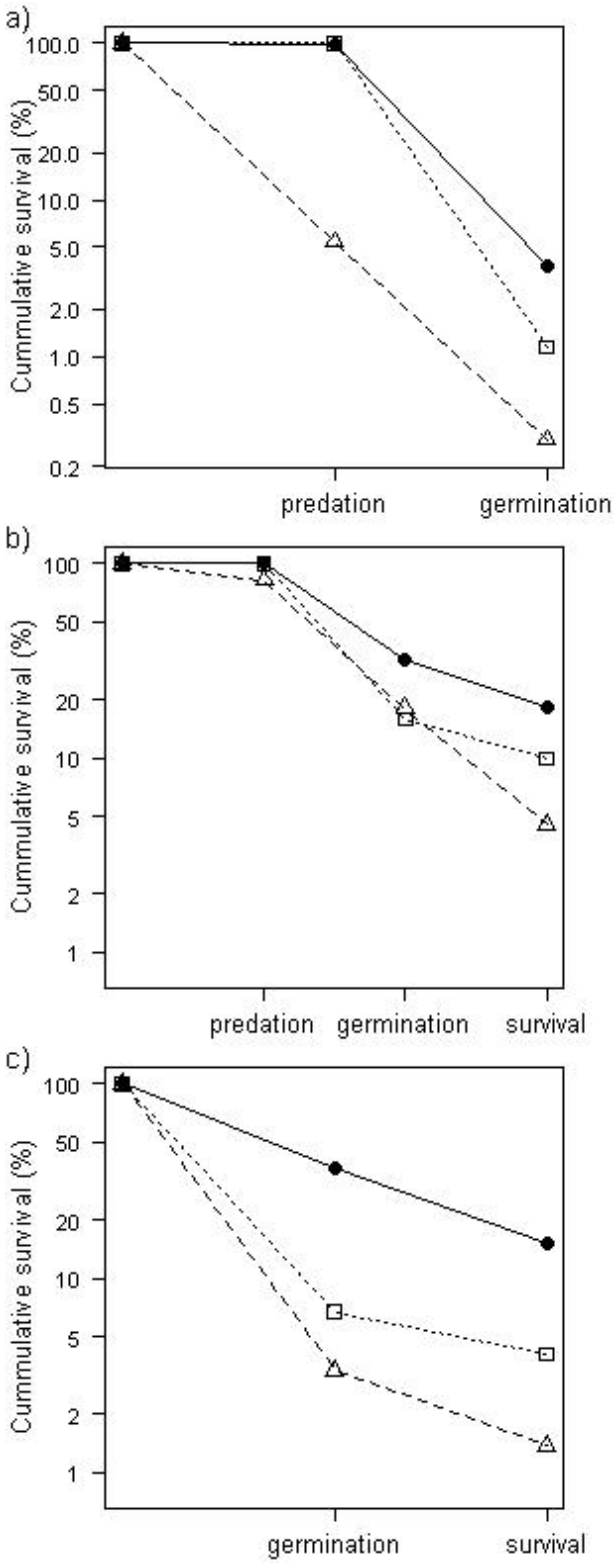

Figure 5.8 Effect of dispersal failure and introduced mammals on survival of a) *E. hookerianus*, b) *R. scandens* and c) *C. robusta.* Mean cumulative survival rates (GLMM fitted values) are plotted through different recruitment stages (post-dispersal seed predation, germination, and seedling survival). Filled circles: best-case scenario ("dispersed" and introduced mammals excluded); squares: dispersal failure ("undispersed" and mammals excluded); triangles: worst-case scenario ("undispersed" and mammals present). Treatment levels for "dispersed" were clean seeds, away from conspecific, and low density. Treatment levels for "undispersed" were whole fruits, under conspecific, and high density. Note the y-axis log scale.

Discussion

By using manipulative field-based experiments, I found that recruitment in three plant species is affected by dispersal failure and introduced mammalian seed and seedling predators. Excluding mammals increased survival in a range of recruitment stages, particularly the seed predation stage, while fruit pulp removal was beneficial mainly through decreasing seed predation. There was little evidence for density- or distance-dependent effects in these plant species.

The Janzen-Connell hypothesis predicts that mortality of seeds and seedlings will decrease with increasing distance from parent trees, due to distance- or density-dependent host-specific enemies (Janzen 1970; Connell 1971). If Janzen-Connell effects were operating, seed predation or seed and seedling mortality should be higher under than away from parent plants, or at high density than low density. In addition, I would expect higher seedling emergence or survival away from than under parent plants, or at low density than high density. However, the only result consistent with the Janzen-Connell hypothesis was the higher seedling emergence of *C. robusta* at low density than high density. Since there was no exclosure × density interaction for *C. robusta*, the lower emergence at high seed density could be due to either increased insect predation or intraspecific competition, or both. *Coprosma robusta* seeds are known to incur a low level of insect attack (Sullivan *et al.* 1995), which could be heightened at high density, or seeds may compete for a common limiting resource such as water or nutrients (Vilà & Sardans 1999; Terborgh 2012).

In contrast to other studies, I did not find any significant effects of distance from parent plant on recruitment. Wotton and Kelly (2011) found that movement away from the parent and fruit pulp removal were the dominant factors affecting *Beilschmiedia tarairi* survival, and for *Corynocarpus laevigatus*, movement away from parents had the greatest effect, increasing survival at all recruitment stages. A worldwide review by Carson *et al.* (2008) on studies explicitly testing the Janzen-Connell hypothesis found that distance and/or density effects are recurrent across studies; common in the tropics, but under-evaluated in temperate ecosystems. In a review focused largely (but not exclusively) on Amazonian studies, Terborgh (2012) found that when density and distance effects are isolated, distance effects are more common than density effects. Terborgh (2012) claimed that bi-trophic interactions (interactions between seed/seedling predators and plants), rather than intraspecific competition between propagules, are the main mechanism for Janzen-Connell effects. I expected seed predation of *E. hookerianus* to be higher under than away from parent trees, due to the large seed crops that build up beneath *E. hookerianus* trees (pers. obs.). In contrast, *R. scandens* twines up and across multiple plants, spreading throughout the forest, rather

than producing a single canopy from which seeds fall to the ground, so there is not a clear signal to guide foraging. However, distance was not an important factor for either plant species.

The exclusion of mammals had a greater effect on plant survival than did distance or density. Excluding mammals increased the survival of *E. hookerianus* and *R. scandens* seeds at the predation stage, increased the germination of *C. robusta,* and increased the seedling survival of *R. scandens* and *C. robusta.* Mammals clearly have negative impacts on plants at a range of recruitment stages. Connell (1971) stated that attack by natural enemies is the most likely cause of greater seedling mortality near parent trees, and that for this mechanism to be effective, the enemies must be both specialised in their choice of prey and not particularly mobile. He suggested that populations of insects or fungi were likely candidates. Janzen (1970) agreed that distance-responsive predators are primarily insects. The lack of distance-dependent mortality, together with the positive effects of excluding mammals that were observed in this study supports this hypothesis. I observed little insect seed predation, while mammal predation was frequent. Since mammals are highly mobile compared to insects or fungi, this is probably the reason why distance was not an important factor in most cases; seeds and seedlings are affected by mammals whether they are under or away from the parent. Another prediction of the Janzen-Connell hypothesis is host-specificity of the predator. Insects are generally more specialised on a single plant species than vertebrates (Bernays & Graham 1988). Furthermore, all the mammalian herbivores in New Zealand are introduced, which increases their impact as generalist herbivores (Parker *et al.* 2006).

Ship rats and possums were probably responsible for the mammalian seed predation I observed (Beveridge 1964; Berry 2006). Rodents are well known seed predators in New Zealand forests (Williams *et al.* 2000; Wilson *et al.* 2003; Ruscoe *et al.* 2004). Seed predation of *Elaeocarpus dentatus* (congeneric to *E. hookerianus*) and *R. scandens* by ship rats has been recorded (Beveridge 1964). Ship rats typically gnaw through the hard seed coat to extract the kernel (Beveridge 1964). Possums can act as seed predators and seed dispersers (Cowan 1990). Berry (2006) showed that possums are post-dispersal seed predators in nearby Peel Forest Park in south Canterbury. Williams *et al.* (2000) found that over a range of plant species, possums destroyed on average 66% of the seeds they consumed from whole fruits. Possums eat *C. robusta* fruit and can disperse seeds intact, however, germination is low (approximately 30%) compared to bird-dispersed seeds (60-70%) (see Chapter 3). Introduced mammals disrupt plant regeneration both directly through predation of seeds and seedlings (this study; Wilson *et al.* 2003), and indirectly by causing a decline in densities of frugivorous birds through predation and competition (Brown 1993; Clout *et al.* 1995).

Fruit pulp removal was previously thought to be critical for promoting germination. Studies by Burrows (1995c; 1996a; 1996f; 1999b) showed many New Zealand plant species failing to germinate

from whole fruits. This raised concern that seeds would die before germinating if they were not ingested by a frugivore. Robertson *et al.* (2006) later found this lack of germination to be an artefact of using Petri dishes for the germination trials, presumably preventing inhibitors to naturally leach away as they would in the field. In subsequent field experiments, germination of a range of large-seeded New Zealand plant species was statistically significantly higher from clean seeds than whole fruits, however, the difference was biologically small (mean 65.5% versus 58.6%) (Kelly *et al.* 2010). I found that fruit pulp removal increased the germination of *R. scandens* and *C. robusta* by approximately 20% (from 18 to 38% for *R. scandens*, and from 5 to 24% for *C. robusta*), which could be due to higher seed predation of whole fruits (for *C. robusta*), higher levels of pathogens and fungi that can occur in whole fruits, or elimination of germination inhibitors present in the fruit pulp (Traveset 1998). However, if seedling emergence was monitored for a longer time period, the differences in germination between whole fruits and clean seeds may reduce. If un-germinated seeds in fruits are merely dormant, they may germinate later and a delay in germination may have no cost to the plant, or may even serve as a conditional strategy for dispersal in time (Kelly *et al.* 2004). Kelly *et al.* (2010) measured seedling emergence of *R. scandens* (among other species) in the field for whole fruits and clean seeds and in one trial 99% of the seeds from whole fruits that germinated did so after 14 months (compared to 100% of clean seeds), while the last seed to germinate did so after 2 years (J.J. Ladley pers. comm.). I monitored *R. scandens* germination for 21 months, however, some new seedlings (from both whole fruits and clean seeds) were still appearing at the final count, so it is likely that at least a small amount of germination will continue.

Germination of *E. hookerianus* certainly requires a longer monitoring period. Kelly *et al.* (2010) found that germination of *Elaeocarpus dentatus* had restricted germination with long delays before first germination, similar to the pattern found here for *E. hookerianus. Elaeocarpus dentatus* is one of the four native species with very thick endocarps that Thorsen *et al.* (2009) proposed was for protection against damage in moa gizzards, along with *Vitex lucens*, *Prumnopitys taxifolia* and *P. ferruginea*. Perhaps the poor germination I found in *E. hookerianus* is the result of a similar adaptation to dispersal by moa, which are known to have eaten *E. hookerianus* fruit (Burrows *et al.* 1981; Wood 2007; Lee *et al.* 2010), and this plant species should be added to the list of putatively moa-adapted seeds.

Perhaps the more important effect of fruit removal is in decreasing seed predation. This effect was found for *R. scandens*, and interacted synergistically with caging for *E. hookerianus* (significant exclosure × fruit interaction). The presence of fruit pulp causing increased seed predation has previously been shown for New Zealand plant species (Wotton & Kelly 2011). Moles and Drake (1999) reported that removal rates of *R. scandens* whole fruits were 3.3 times higher than for clean

seeds, and suggested that seed predators may use the fruit pulp as olfactory or visual cues when foraging.

Two other major benefits of dispersal that were not quantified in this study are the colonisation of new sites and maintenance of meta-population dynamics. Seeds swallowed by frugivores have a higher chance of being moved to distant sites, thus increasing gene flow between populations and potentially avoiding inbreeding depression (García *et al.* 2007; Robertson *et al.* 2011). Therefore, even if the transport of seeds away from parents is not necessary for seed or seedling survival at a local scale, it may still be necessary for population persistence at a broader landscape scale. This area requires further research however, as we have little idea of how much longer-distance dispersal is necessary for the maintenance of meta-populations (Kelly *et al.* 2010).

My study is one of a few that have experimentally demonstrated that recruitment of undispersed seeds is lower than dispersed seeds (Christian 2001; Wotton & Kelly 2011), rather than inferring a detrimental effect of dispersal failure on recruitment using comparative methods (Chapman & Chapman 1995; Terborgh *et al.* 2008; Sethi & Howe 2009). When mammals were excluded, the surviving seedling density from dispersed compared with undispersed seeds was 4% versus 1% for *E. hookerianus*; 18% versus 10% for *R. scandens*, and 15% versus 4% for *C. robusta.* Introduced mammals further decreased survival (to 0.3%, 5%, and 1%). This study supports the growing evidence of detrimental effects of introduced mammals on plant recruitment and the importance of maintaining bird-plant seed dispersal mutualisms, in this case partly for the protection that bird dispersers confer against introduced seed and seedling predators.

Chapter 6: Synthesis

Kereru resting in *Vitex lucens* (puriri). Photo: T. Wyman.

The main objective of this thesis was to determine the effects of bird declines on seed dispersal and to assess the current status of dispersal in New Zealand. In this chapter I synthesise my main findings in relation to these aims, and discuss their implications for conservation and future research.

Effects of bird declines and introduced mammals on seed dispersal

Human influence has greatly reduced the density and diversity of native birds throughout New Zealand, but depleted avifaunas are not unique to this country. Worldwide declines in bird numbers have sparked interest in how well bird-plant mutualisms such as seed dispersal are functioning (Sekercioglu *et al.* 2004), and understanding the consequences of the loss of native mutualists highlights the importance of those remaining. I investigated the effects of bird declines on the level of dispersal service plants receive (Chapter 2), and whether poor dispersal service would actually result in lower plant recruitment (Chapter 5). My results suggest that there is a positive correlation between dispersal service and bird density, with plants receiving better dispersal service at high bird sites. When bird density is reduced, low-reward plant species are at most risk of dispersal failure. Non-dispersal results in whole fruits dropped in high densities below parent trees that are more vulnerable to mammalian seed and seedling predators. This translates to a direct decrease in plant recruitment, so there is a real cost to the plant resulting from reduced bird abundance. Luckily, it appears that New Zealand suffers from weaker Janzen-Connell effects than often observed overseas. The "strong" version of the Janzen-Connell hypothesis includes a "death zone" under the parent where survival is virtually zero (Bagchi *et al.* 2010), whereas in New Zealand such effects are weaker (though significant; Wotton & Kelly 2011; Jana 2012). My study presented in Chapter 5 would have benefited had I been able to assess the viability of ungerminated seeds at the end of the experiment, but logistical difficulties prevented this. Future studies should aim to do so in order to provide the clearest results, as it is valuable to know whether remaining seeds are dead or dormant. The very slow and restricted germination found here and in Kelly *et al.* (2010) for some species such as *Elaeocarpus hookerianus*, makes it difficult to finish these experiments within the duration of a PhD study. Monitoring is planned to continue for *E. hookerianus* so that final seedling emergence and survival can be reported in the future.

Introduced mammals are increasingly being considered as potential dispersers of native and exotic seeds in New Zealand. Seed dispersal by introduced mammals has been recorded for species such as possums, rodents, pigs, sheep, and rabbits (Williams *et al.* 2000; Dungan *et al.* 2002; O'Connor & Kelly 2012; Young 2012). While it is clear that most mammals eat fruit at least occasionally, the negative effects of mammal fruit consumption will often outweigh the benefits

received. An example is seed dispersal by possums as shown in Chapter 3. Although possums disperse some seeds, many of those consumed are destroyed or have lower germination than those dispersed by birds. In addition to the decrease in recruitment resulting from non-dispersal by birds, there may also be an indirect cost to the plant from having seeds dispersed by alternative, but less effective dispersers. Not all native 'dispersers' necessarily provide a net benefit either. For example, the consumption of small fruits by tree weta, whereby the lack of movement and low survival rate of seeds consumed by weta replaces the high-quality dispersal of birds with low-quality dispersal (Wyman *et al.* 2011). Worse than being less effective dispersers, rodents will often kill seeds outright without giving any seed dispersal benefit at all (Beveridge 1964; Towns *et al.* 2006). These negative effects, in addition to direct predation on birds (Moors 1983; Brown *et al.* 1998), are unlikely to outweigh any small contribution to seed dispersal by introduced mammals.

Sometimes a lack of regeneration may appear to be the result of poor dispersal service, but may actually be cryptic predation. In these instances, the use of experimental manipulations such as the mammal-proof exclosures used in my study (Chapter 5), is useful to distinguish the effects of non-dispersal from seed or seedling predation (Wilson *et al.* 2003; Wotton & Kelly 2011). In another example, after fire destroyed forest of the Awarua Waituna wetland, the New Zealand Department of Conservation assumed that the lack of regeneration was due to a lack of seed sources and dispersal limitation, and that mammals were scarce in the area. However, seed sowing and mammal exclosure treatments are showing that by far the biggest impediment to recruitment is seed and seedling predation, with very low seedling survival when seeds are not protected by cages (O.R. Burge, pers. comm.). In cases like these, increasing the seed input will have little effect if the majority of those seeds are subsequently predated, and protection of seedlings from mammals; either through control or fencing, may be the most beneficial management option. Studies combining both observational and manipulative experiments (cf. Wenny 2000) are invaluable in this sense.

As shown in Chapter 5, the loss of bird dispersal negatively affects plants in terms of recruitment, and the combined loss of dispersal plus seed predation by mammals is a worst-case scenario for regeneration (Wotton & Kelly 2011). Of course, on the New Zealand mainland, the loss of dispersal is almost always accompanied by the presence of introduced mammals, while offshore islands that are free of introduced mammals are often having much improved trajectories (Bellingham *et al.* 2010).

Current status of seed dispersal in New Zealand

There have been few studies documenting dispersal quantity for New Zealand plant species. Studies of seed dispersal service to mistletoes (*Peraxilla colensoi, P. tetrapetala*, *Alepis flavida*, *Tupeia antarctica*, and *Ileostylus micranthus*) showed that while dispersal is adequate in most seasons, it can be limited in others (Ladley & Kelly 1996; Kelly *et al.* 2004). Kelly *et al.* (2010) list the studies documenting dispersal quantity of New Zealand plant species. In addition to the mistletoes mentioned above, five species have been studied, of which two showed good dispersal (*Beilschmiedia tawa* and *Prumnopitys ferruginea*), two showed slow dispersal (*Rhopalostylis sapida* and *Fuchsia excorticata*), and one showed poor dispersal (*Pittosporum crassifolium*). The two species that showed good dispersal (*B. tawa* and *P. ferruginea*) were confirmed to be receiving good dispersal in my study. In addition, I can add three more species (*Elaeocarpus dentatus*, *Melicytus ramiflorus*, and *Coprosma robusta*) to the list of those receiving good dispersal service. I can also add a second species (*Coprosma areolata*) to those receiving poor dispersal service (at least at one site). Including mistletoes, that makes ten species showing good dispersal (in most seasons), two showing slow dispersal, and two showing poor dispersal. Overall then, it appears that most plant species are getting most fruits removed most of the time. This is in contrast to pollination in New Zealand, where there is evidence for widespread pollen limitation in the majority of species studied with ornithophilous flowers (Kelly *et al.* 2010).

Introduced birds were considered to contribute little to dispersal of native plants in New Zealand (Williams & Karl 1996; Kelly *et al.* 2006), and blackbirds have been associated with the spread of weeds (Williams 2006). My research (Chapter 3) showed that blackbirds and song thrushes dispersed high numbers of seeds per faecal deposit (similar quantities to bellbirds and silvereyes) and the majority of these were native plant species. After correcting for the lower mist netting catch rate of these birds by using estimates of abundance, these introduced birds accounted for approximately 60% of total dispersal. These results are consistent with other recent studies showing that blackbirds and song thrushes are important dispersers of native plants. O'Connor (2012) studied dispersal of *Prumnopitys taxifolia* and found that blackbirds and song thrushes combined contributed 22% of the feeding visits. Burns (2012) showed that blackbirds were among the most common frugivores in Karori Wildlife Sanctuary, Wellington ('Zealandia'), and after correcting for sampling effort, blackbirds exhibited similar levels of dietary diversity to native bird species at Zealandia, as well as at a Westland forest in the South Island (O'Donnell & Dilks 1994).

These data suggest that even though introduced birds such as blackbirds and song thrushes share no evolutionary history with the New Zealand flora, they have rapidly developed important

relationships with native plants as frugivores. This is consistent with the theory that animal-mediated seed dispersal is a diffuse mutualism, in which animals are able to feed on a range of novel fruit species without the requirement of a coevolutionary history. This is good news for seed dispersal as it appears that these introduced birds may provide effective seed dispersal services supplementary to those made by remaining native birds. The exception is dispersal of the very largest-seeded plant species, for which kereru are essential (Wotton & Kelly 2011).

Future work may benefit from investigations of whether introduced birds compete with native birds for food resources or habitat. However, O'Connor (2012) never observed an introduced bird attacking or chasing a native bird, while on four occasions, a native bird (bellbird or kereru) was seen chasing an introduced bird (blackbird or song thrush), and she therefore concluded that in her study site introduced birds did not have a negative effect on the behaviour of native birds. It may also be of interest to investigate whether native plants are beginning to show any adaptations to dispersal by introduced birds. For example, if introduced birds more effectively dispersed smaller seeds this could lead to selection in the characteristics of the fruit changing over time. A recent study documented rapid reduction in seed size of a palm due to functional extinction of large-gaped birds within the past 100 years (Galetti *et al.* 2013). However, there may be little directional selection for smaller fruits in New Zealand as long as kereru are present in sufficient densities to provide adequate dispersal of large fruits. Furthermore, the general lack of evidence of dispersal failure here suggests little selection pressure. Also, kereru are generally not gape-limited and fruit size preferences appear to be independent of mean fruit size (Wotton & Ladley 2008).

Introduced bird frugivores interact positively with native plants through seed dispersal, while introduced mammals such as possums negatively affect native plants. This is in agreement with the results of a worldwide meta-analysis comparing the effectiveness of pollination and seed dispersal functions of native and non-native vertebrates (Aslan *et al.* 2012). Non-native mutualists were significantly less effective than native mutualists when the taxonomic class of the mutualists differed (either bird or mammal). However, native and non-native mutualists in the same taxonomic group did not differ significantly in effectiveness (Aslan *et al.* 2012). The digestive tracts of mammals may be more likely to damage seeds than the digestive tracts of birds (Traveset 1998; but see Verdu & Traveset 2004). Since New Zealand's flora evolved in the absence of non-flying mammals, seeds may be largely adapted to the more gentle gut passage of birds, which may account for some of the difference in dispersal effectiveness of introduced birds versus mammals (e.g. low germination percentage of possum-dispersed *C. robusta* seeds compared to bird-dispersed seeds). Although a few large-seeded species (*Vitex lucens*, *Prumnopitys taxifolia*, *P. ferruginea*, *Elaeocarpus dentatus*) have thickened endocarps, which are possibly adapted for protection from moa gizzard action

(Thorsen *et al.* 2009; Kelly *et al.* 2010, Chapter 5), these fruits are for the most part too large for dispersal by introduced mammals (Williams 2003).

Conservation implications

So if seed dispersal is still mostly functioning adequately in New Zealand, will it stay this way in the future? A primary driver of how well bird-plant interactions function is the range and density of avian mutualists. Although suffering from declines in density and range since human colonisation in the last c. 800 years, according to *Robertson et al.* (2007), the trend for the primary dispersing birds (kereru, tui, bellbird and silvereye) is looking positive (although 25/66 endemic birds are still declining). Kereru, tui and bellbirds have all increased in distribution since the last atlas (Bull *et al.* 1985), while silvereyes show no change (along with blackbirds, song thrushes, and starlings). Robertson *et al.* (2007) note that some of this increase may be due to better survey coverage in the later atlas, while some may be a feature of reduced competition and predation resulting from possum control. Other evidence for native bird increases comes from Brockie & Duncan (2012), who showed that the number of most native bird species counted along a transect through Wellington city rose substantially between 1989 and 2006. They attributed the increase to an extensive possum and rat control programme that began throughout the Wellington district in the 1990s, and to the establishment of the nearby Karori Wildlife Sanctuary (Zealandia) in 1999.

However, we should not become complacent about the continued conservation of native flora and fauna. As well as protecting birds for their intrinsic value, they are vital for maintaining healthy and functioning ecosystems. Faced with New Zealand's biodiversity crisis, conservation managers and scientists have developed innovative techniques such as translocation of native animals and the eradication of introduced mammals from islands and mainland islands. In the last decade, intensive control of introduced mammalian pests, especially possums, stoats and ship rats, has frequently increased native bird numbers, including tui, bellbird and kereru (Innes *et al.* 1999; Innes *et al.* 2004; Kelly *et al.* 2005; Innes *et al.* 2010; O'Donnell & Hoare 2012). Management can also improve bird-plant mutualisms. Eradication of pests from within a predator-proof fence enclosing Maungatautari Sanctuary and subsequent increases in bird numbers have improved pollination and dispersal mutualisms (Iles 2012). Pest control or eradication can also directly benefit native plants by decreasing consumption of vegetative or reproductive parts by mammals (Cowan 1991; Wilson *et al.* 2006). If pest control were to be relaxed we would certainly see some, if not all of the good work undone. Furthermore, there may be a threshold abundance below which dispersal effectiveness becomes disproportionately low due to a lack of inter- or intraspecific competition. For example,

flying foxes in Tonga cease to function as seed dispersers long before they become rare, due to a lack of aggressive interactions whereby animals in fruiting trees repel newcomers who may snatch a fruit to eat elsewhere, thus dispersing the seeds (McConkey & Drake 2006). The extent of these sorts of non-linear relationships between animal density and the level of service provided remains unknown, but if present could mean that even a small drop in current bird densities could have disproportionately large reductions in dispersal or pollination service. My results from Chapter 2 show a kind of non-linear response depending on fruit sugar levels. Aggressive interactions are known to occur both within and between some native species, for example, tui readily displace bellbirds from food sites (Craig *et al.* 1981; Ladley & Kelly 1996). Since tui were largely absent at my study sites, it would be of interest to compare dispersal service in areas where tui are absent versus present (Canterbury and elsewhere); where bellbirds are absent versus present (Northland and elsewhere); and where both species overlap in range.

New Zealand's original forest is now largely reduced to isolated patches within an agricultural matrix, and the maintenance of native biodiversity within these landscapes relies heavily on the protection and enhancement of the forest remnants (Burns *et al.* 2000). Forest remnants serve as seed sources and provide corridors for animal movement (Miller 2002). An ability to disperse seeds between fragments provides for continued gene flow in the long term. Isolated remnants may suffer reduced dispersal because birds are unwilling to cross open areas to get to them (Corlett 2007; Richard & Armstrong 2010). Moreover, smaller frugivores are generally less mobile and have shorter gut passage times than larger ones such as kereru (Wotton & Kelly 2012), so fewer dispersers are able to provide long-distance dispersal to and from the most isolated fragments. In addition to possum, rodent and mustelid control, isolated forest remnants should ideally be fenced to exclude large ungulates that browse seedlings and saplings. Dispersal service may be adequate, but if the undergrowth is cleared out by these herbivores, regeneration will be limited. I observed stray cows roaming in Kaituna Valley (a supposedly fenced reserve) and this site had a bare undergrowth with few seedlings relative to other study sites.

Kelly *et al.* (2010) have reported widespread pollen limitation in species with ornithophilous flowers. There is an obvious link between pollination and seed dispersal since pollination limitation can lead to reduced fruit and seed set (Montgomery *et al.* 2001). Furthermore, seed dispersal and pollination in New Zealand are often provided by the same animals (tui, bellbird and silvereye; Kelly *et al.* 2006). Pollen limitation can also reduce offspring quality through increased inbreeding or from reduced pollen competition when less pollen is deposited on each stigma (Colling *et al.* 2004). Robertson *et al.* (2011) showed that selfed *Fuchsia excorticata* and *Sophora microphylla* seeds exhibit high levels of inbreeding depression, with very low survival of seedlings, so outcrossing is

necessary for adult replacement. They concluded that "fruit, seed, and seedling production are not reliable indicators of successful recruitment: a high density of doomed selfed offspring can mask the absence of the outcrossed seedlings needed for adult replacement" (p 191). The same may be said for dispersal quantity: a high level of dispersal service may not equate to successful recruitment if those seeds are doomed. I observed a much lower germination in the glasshouse for clean seeds of *Ripogonum scandens* (38%) and *Coprosma robusta* (72%) than Burrows (1995d; 1996e) found for *R. scandens* (88%) and *C. robusta* (92%), also sown in the glasshouse. My seed sets were collected from different sites than Burrows' studies (though all were from the Banks Peninsula region). One possible (though highly speculative) explanation for my low germination is inbreeding depression. My *R. scandens* and *C. robusta* seeds were collected in different years, but both had lower germination than Burrows, so a chance year effect seems unlikely.

Of the 1889 New Zealand seed plants (excluding species that occur only on the Kermadec, Chatham, and subantarctic Islands), bird-visited flowers occur in 85 species (Kelly *et al.* 2010). I surveyed these 85 species and determined how many also have fleshy fruits, and found that 44 do (2.3% of seed plant flora; Table 6.1). These 44 plants depend on birds for both pollination and dispersal. Most of the country has a maximum of three birds that are effective dispersers and pollinators (tui, bellbird and silvereye), but often only two or one of these are present (Robertson *et al.* 2007). I suggest these plants that are both dispersed and pollinated by birds are at a higher risk of reproductive failure due to reduced bird densities, and propose that these plant species should be studied in the future, particularly those that currently show either a pollen or dispersal limitation. So far, pollen limitation has been identified in 5 of the 6 species tested, and slow or poor dispersal in 3 of the 8 species tested (Table 6.1). Both pollen limitation and slow dispersal service occurs in *Fuchsia excorticata*, with selfed seeds exhibiting strong inbreeding depression (Robertson *et al.* 2011). This species is also seed limited, so there is a direct risk of reduced regeneration (Bell 2010).

Table 6.1 New Zealand plant species with bird-visited flowers and fleshy fruits, and outcome of studies on pollination and dispersal service (following Kelly *et al.* 2010).

		Pollen limitation?		
		yes	no	not tested
Dispersal limitation?	yes	*Fuchsia excorticata*		*Pittosporum crassifolium, Rhopalostylis sapida*
	no	*Peraxilla colensoi, P. tetrapetala*	*Alepis flavida*	*Beilschmiedia tawa, Elaeocarpus dentatus*
	not tested	*Alseuosmia macrophylla, Fuchsia perscandens*		*Aristotelia serrata, Astelia spp., Beilschmiedia tarairi, Carpodetus serratus, Cordyline australis, Corynocarpus laevigatus, Freycinetia baueriana, Griselinia littoralis, Hedycarya arborea, Leucopogon fasciculatus, Lophomyrtus spp., Melicytus ramiflorus, Myoporum laetum, Myrsine australis, M. salicina, Nestegis lanceolata, Passiflora tetrandra, Pennantia corymbosa, Pittosporum cornifolium, P. eugenioides, P. tenuifolium, P. umbellatum, Pseudopanax arboreus, P. colensoi, P. crassifolius, Pseudowintera colorata, Raukaua simplex, Ripogonum scandens, Rubus cissoids, Schefflera digitata, Syzygium maire, Toronia toru, Trilepidea adamsii, Vitex lucens*

This thesis has provided additional information about the functioning of seed dispersal in today's modified ecosystems. With our current information, it appears most native plants are receiving adequate dispersal, despite the reduced bird densities and ongoing negative effects of introduced mammals in New Zealand. However, the information is still limited. With studies on only a few plant species, we have only touched the surface (Table 6.1). While some non-native species may provide some buffer against the loss of native birds, the function of native dispersers cannot be fully replaced. For the continued health and survival of remaining ecosystems, it is vital that mutualistic processes like seed dispersal continue to function effectively.

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References

Allan Herbarium (2000) New Zealand Plant Names Database. Landcare Research, New Zealand. http://nzflora.landcareresearch.co.nz/.

Anderson, S. (1997) Changes in native ecosystem processes: the dynamics of pollination and dispersal in New Zealand forest. MSc thesis, University of Auckland, New Zealand.

Anderson, S.H., Kelly, D., Ladley, J.J., Molloy, S. & Terry, J. (2011) Cascading effects of bird functional extinction reduce pollination and plant density. *Science,* **331,** 1068-1071.

Anderson, S.H., Kelly, D., Robertson, A.W., Ladley, J.J. & Innes, J. (2006) Birds as pollinators and dispersers: a case study from New Zealand. *Acta Zoologica Sinica,* **52 (Supplement),** 112-115.

Aslan, C.E., Zavaleta, E.S., Croll, D. & Tershy, B. (2012) Effects of native and non-native vertebrate mutualists on plants. *Conservation Biology,* **26,** 778-789.

Atkinson, I.A.E., Campbell, D.J., Fitzgerald, B.M., Flux, J.E.C. & Meads, M.J. (1995) Possums and possum control: effects on lowland forest ecosystems. *Science for Conservation*. Department of Conservation, Wellington, New Zealand.

Augspurger, C.K. (1983) Seed dispersal of the tropical tree, *Platypodium elegans*, and the escape of its seedlings from fungal pathogens. *Journal of Ecology,* **71,** 759-771.

Bagchi, R., Swinfield, T., Gallery, R.E., Lewis, O.T., Gripenberg, S., Narayan, L. & Freckleton, R.P. (2010) Testing the Janzen-Connell mechanism: pathogens cause overcompensating density dependence in a tropical tree. *Ecology Letters,* **13,** 1262-1269.

Barker, R. (2009) The treasures of Prices Valley. *Land Notes*, pp. 5. Banks Peninsula Conservation Trust, Christchurch, New Zealand.

Bass, D.A. (1990) Dispersal of an introduced shrub (*Crataegus monogyna*) by the brushtailed possum (*Trichosurus vulpecula*). *Australian Journal of Ecology,* **15,** 227-229.

Bates, D., Maechler, M. & Bolker, B. (2013) lme4: Linear mixed-effects models using S4 classes. R package version 0.999999-2. http://CRAN.R-project.org/package=lme4.

Beavon, M. (2007) Pollination and dispersal of the noxious vine *Passiflora mollissima*. MSc thesis, University of Canterbury, New Zealand.

Bell, R.J.H. (2010) Is *Fuchsia excorticata* (Onagraceae) seed limited? PhD thesis, University of Canterbury, New Zealand.

Bellingham, P.J., Towns, D.R., Cameron, E.K., Davis, J.J., Wardle, D.A., Wilmshurst, J.M. & Mulder, C.P.H. (2010) New Zealand island restoration: seabirds, predators, and the importance of history. *New Zealand Journal of Ecology,* **34,** 115-136.

Bergquist, C.A.L. (1985) Movements of groups of tui (*Prosthemadera novaeseelandiae*) in winter and settlement of juvenile tui in summer. *New Zealand Journal of Zoology,* **12,** 569-571.

Bernays, E. & Graham, M. (1988) On the evolution of host specificity in phytophagous arthropods. *Ecology,* **69,** 886-892.

Berry, C.J.J. (2006) Post-dispersal seed predation in a conifer-broadleaf forest remnant: the importance of exotic mammals. PhD thesis, Lincoln University, New Zealand.

Beveridge, A.E. (1964) Dispersal and destruction of seed in central North Island podocarp forests. *Proceedings of the New Zealand Ecological Society,* **11,** 48-56.

Beveridge, A.E. (1973) Regeneration of podocarps in a central North Island forest. *New Zealand Journal of Forestry,* **18,** 23-35.

Bleher, B. & Böhning-Gaese, K. (2001) Consequences of frugivore diversity for seed dispersal, seedling establishment and the spatial pattern of seedlings and trees. *Oecologia,* **129,** 385-394.

Bluthgen, N., Menzel, F. & Bluthgen, N. (2006) Measuring specialization in species interaction networks. *BMC Ecology,* **6,** 9.

Bond, W.J. (1994) Do mutualisms matter? Assessing the impact of pollinator and disperser disruption on plant extinction. *Philosophical Transactions: Biological Sciences,* **344,** 83-90.

Booth, D.F. (1984) Classified summarised notes. *Notornis,* **31,** 40-85.

Boyer, A.G. (2010) Consistent ecological selectivity through time in Pacific island avian extinctions. *Conservation Biology,* **24,** 511-519.

Brockie, R.E. & Duncan, C. (2012) Long term trends in Wellington City bird counts: 1969-2006. *Notornis,* **59,** 1-6.

Brodie, J.F., Helmy, O.E., Brockelman, W.Y. & Maron, J.L. (2009) Bushmeat poaching reduces the seed dispersal and population growth rate of a mammal-dispersed tree. *Ecological Applications,* **19,** 854-863.

Brown, K. (1993) Evidence that possums prey on and scavenge birds' eggs, birds and mammals. *Notornis,* **40,** 169-177.

Brown, K., Moller, H., Innes, J. & Jansen, P. (1998) Identifying predators at nests of small birds in a New Zealand forest. *Ibis,* **140,** 274-279.

Bull, P.C., Gaze, P.D. & Robertson, C.J.R. (1985) *The atlas of bird distribution in New Zealand*. Ornithological Society of New Zealand, Wellington, New Zealand.

Burns, B., Barker, G.M., Harris, R. & Innes, J. (2000) Conifers and cows: forest survival in a New Zealand dairy landscape. *Conservation in production environments: managing the matrix* (eds J.L. Craig, D.A. Saunders & N. Mitchell), pp. 81-89. Surrey Beatty & Sons, Chipping Norton, Australia.

Burns, K.C. (2012) Are introduced birds unimportant mutualists? A case study of frugivory in European blackbirds (*Turdus merula*). *New Zealand Journal of Ecology,* **36,** 1-6.

Burrows, C.J. (1995a) Germination behaviour of seeds of the New Zealand species *Fuchsia excorticata*, *Griselinia littoralis*, *Macropiper excelsum*, and *Melicytus ramiflorus*. *New Zealand Journal of Botany,* **33,** 131-140.

Burrows, C.J. (1995b) Germination behaviour of the seeds of 4 New Zealand species of *Coriaria* (Coriariaceae). *New Zealand Journal of Botany,* **33,** 265-275.

Burrows, C.J. (1995c) Germination behaviour of the seeds of 6 New Zealand woody plant species. *New Zealand Journal of Botany,* **33,** 365-377.

Burrows, C.J. (1995d) Germination behaviour of the seeds of the New Zealand species *Aristotelia serrata*, *Coprosma robusta*, *Cordyline australis*, *Myrtus obcordata*, and *Schefflera digitata*. *New Zealand Journal of Botany,* **33,** 257-264.

Burrows, C.J. (1996a) Germination behaviour of seeds of the New Zealand woody species *Alectryon excelsus*, *Corynocarpus laevigatus*, and *Kunzea ericoides*. *New Zealand Journal of Botany,* **34,** 489-498.

Burrows, C.J. (1996b) Germination behaviour of seeds of the New Zealand woody species *Ascarina lucida*, *Coprosma grandifolia*, *Melicytus lanceolatus*, and *Solanum laciniatum*. *New Zealand Journal of Botany,* **34,** 509-515.

Burrows, C.J. (1996c) Germination behaviour of seeds of the New Zealand woody species *Coprosma foetidissima*, *Freycinetia baueriana*, *Hoheria angustifolia*, and *Myrsine australis*. *New Zealand Journal of Botany,* **34,** 499-508.

Burrows, C.J. (1996d) Germination behaviour of seeds of the New Zealand woody species *Melicope simplex*, *Myoporum laetum*, *Myrsine divaricata*, and *Urtica ferox*. *New Zealand Journal of Botany,* **34,** 205-213.

Burrows, C.J. (1996e) Germination behaviour of the seeds of seven New Zealand vine species. *New Zealand Journal of Botany,* **34,** 93-102.

Burrows, C.J. (1996f) Germination behaviour of the seeds of seven New Zealand woody plant species. *New Zealand Journal of Botany,* **34,** 355-367.

Burrows, C.J. (1999a) Germination behaviour of seeds of the New Zealand woody species *Alseuosmia macrophylla*, *A. pusilla*, *Cordyline banksii*, *Geniostoma rupestre*, *Myrtus bullata*, and *Solanum aviculare*. *New Zealand Journal of Botany,* **37,** 277-287.

Burrows, C.J. (1999b) Germination behaviour of seeds of the New Zealand woody species *Beilschmiedia tawa*, *Dysoxylum spectabile*, *Griselinia lucida*, and *Weinmannia racemosa*. *New Zealand Journal of Botany,* **37,** 95-105.

Burrows, C.J., McCulloch, B. & Trotter, M.M. (1981) *The diet of moas based on gizzard contents samples from Pyramid Valley, North Canterbury, and Scaifes Lagoon, Lake Wanaka, Otago*. Order of the Canterbury Museum Trust Board, Christchurch, New Zealand.

Cain, M.L., Milligan, B.G. & Strand, A.E. (2000) Long-distance seed dispersal in plant populations. *American Journal of Botany,* **87,** 1217-1227.

Campbell, D.J. & Atkinson, I.A.E. (2002) Depression of tree recruitment by the Pacific rat (*Rattus exulans* Peale) on New Zealand's northern offshore islands. *Biological Conservation,* **107,** 19-35.

Carson, W.P., Anderson, J., Leight Jr, E. & Schnitzer, S. (2008) Challenges associated with testing and falsifying the Janzen-Connell hypothesis: a review and critique. *Tropical forest community ecology* (eds W.P. Carson & S.A. Schnitzer), pp. 210-241. Wiley-Blackwell, Malden, MA.

Caves, E.M., Jennings, S.B., HilleRisLambers, J., Tewksbury, J.J. & Rogers, H.S. (2013) Natural experiment demonstrates that bird loss leads to cessation of dispersal of native seeds from intact to degraded forests. *PLOS ONE,* **8,** e65618.

Chapman, C.A. & Chapman, L.J. (1995) Survival without dispersers: seedling recuitment under parents. *Conservation Biology,* **9,** 675-678.

Chimera, C.G. & Drake, D.R. (2010) Patterns of seed dispersal and dispersal failure in a Hawaiian dry forest having only introduced birds. *Biotropica,* **42,** 493-502.

Christian, C.E. (2001) Consequences of a biological invasion reveal the importance of mutualism for plant communities. *Nature,* **413,** 635-639.

Cipollini, M.L. & Levey, D.J. (1997) Secondary metabolites of fleshy vertebrate-dispersed fruits: adaptive hypotheses and implications for seed dispersal. *The American Naturalist,* **150,** 346-372.

Clark, D.A. & Clark, D.B. (1984) Spacing dynamics of a tropical rain forest tree: evaluation of the Janzen-Connell model. *American Naturalist,* **124,** 769-788.

Clark, J.S., Macklin, E. & Wood, L. (1998) Stages and spatial scales of recruitment limitation in southern Appalachian forests. *Ecological Monographs,* **68,** 213-235.

Clark, J.S., Silman, M., Kern, R., Macklin, E. & HilleRisLambers, J. (1999) Seed dispersal near and far: patterns across temperate and tropical forests. *Ecology,* **80,** 1475-1494.

Clout, M. & Gaze, P. (1984) Effects of plantation forestry on birds in New Zealand. *Journal of Applied Ecology,* **21,** 795-815.

Clout, M.N. (2006) Keystone aliens? The multiple impacts of brushtail possums. *Biological Invasions in New Zealand* (eds R.B. Allen & W.G. Lee), pp. 265-279. Springer-Verlag, Berlin, Germany.

Clout, M.N. & Efford, M.G. (1984) Sex differences in the dispersal and settlement of brushtail possums (*Trichosurus vulpecula*). *Journal of Animal Ecology,* **53,** 737-749.

Clout, M.N. & Hay, J.R. (1989) The importance of birds as browsers, pollinators and seed dispersers in New Zealand forests. *New Zealand Journal of Ecology,* **12,** 27-33.

Clout, M.N., Karl, B.J., Pierce, R.J. & Robertson, H.A. (1995) Breeding and survival of New Zealand pigeons *Hemiphaga Novaeseelandiae*. *Ibis,* **137,** 264-271.

Clout, M.N. & Tilley, J.A.V. (1992) Germination of miro (*Prumnopitys ferruginea*) seeds after consumption by New Zealand pigeons (*Hemiphaga novaeseelandiae*). *New Zealand Journal of Botany,* **30,** 25-28.

Coleman, J., Gillman, A. & Green, W. (1980) Forest patterns and possum densities within podocarp/mixed hardwood forests on Mt Bryan O'Lynn, Westland. *New Zealand Journal of Ecology,* **3,** 69-84.

Coleman, J.D., Green, W.Q. & Polson, I.G. (1985) Diet of brushtail possums over a pasture-alpine gradient in Westland, New Zealand. *New Zealand Journal of Ecology,* **8,** 21-35.

Colling, G., Reckinger, C. & Matthies, D. (2004) Effects of pollen quantity and quality on reproduction and offspring vigor in the rare plant *Scorzonera humilis* (Asteraceae). *American Journal of Botany,* **91,** 1774-1782.

Colwell, R.K. (2009) EstimateS: Statistical estimation of species richness and shared species from samples. http://viceroy.eeb.uconn.edu/estimates/.

Connell, J.H. (1971) On the role of natural enemies in preventing competitive exclusion in some marine animals and in rainforest trees. *Dynamics of populations* (eds P.J. Den Boer & G. Gradwell), pp. 298-312. PUDOC, Wageningen, Netherlands.

Cordeiro, N.J. & Howe, H.F. (2003) Forest fragmentation severs mutualism between seed dispersers and an endemic African tree. *Proceedings of the National Academy of Sciences,* **100,** 14052-14056.

Corlett, R.T. (1998) Frugivory and seed dispersal by vertebrates in the Oriental (Indomalayan) Region. *Biological Reviews,* **73,** 413-448.

Corlett, R.T. (2007) Pollination or seed dispersal: which should we worry about most? *Seed Dispersal: Theory and its Application in a Changing World* (eds A.J. Dennis, E.W. Schupp, R.J. Green & D.A. Westcott), pp. 523-544. CABI, Wallingford, UK.

Cowan, P. & Clout, M. (2000) Possums on the move: activity patterns, home ranges, and dispersal. *The brushtail possum: biology, impact and management of an introduced marsupial* (ed. T.L. Montague), pp. 24-34. Manaaki Whenua Press, Lincoln, New Zealand.

Cowan, P.E. (1990) Fruits, seeds, and flowers in the diet of brushtail possums, *Trichosurus vulpecula*, in lowland podocarp mixed hardwood forest, Orongorongo Valley, New Zealand. *New Zealand Journal of Zoology,* **17,** 549-566.

Cowan, P.E. (1991) Effects of introduced Australian brushtail possums (*Trichosurus vulpecula*) on the fruiting of the endemic New Zealand nikau palm (*Rhopalostylis sapida*). *New Zealand Journal of Botany,* **29,** 91-93.

Cowan, P.E. (1992) Analysis of the characteristics of fruit eaten by possums, *Trichosurus vulpecula*, in New Zealand. *New Zealand Journal of Zoology,* **19,** 45-52.

Cowan, P.E. & Waddington, D.C. (1990) Suppression of fruit production of the endemic forest tree, *Elaeocarpus dentatus*, by introduced marsupial brushtail possums, *Trichosurus vulpecula*. *New Zealand Journal of Botany,* **28,** 217-224.

Craig, J.L., Stewart, A.M. & Douglas, M.E. (1981) The foraging of New Zealand honeyeaters. *New Zealand Journal of Zoology,* **8,** 87-91.

Daniel, M.J. (1973) Seasonal diet of the ship rat (*Rattus r. rattus*) in a lowland forest in New Zealand. *Proceedings of the New Zealand Ecological Society,* **20,** 21–30.

Daugherty, C.H., Gibbs, G.W. & Hitchmough, R.A. (1993) Mega-island or micro-continent? New Zealand and its fauna. *Trends in Ecology & Evolution,* **8,** 437-442.

Dawson, D.G. & Bull, P.C. (1975) Counting birds in New Zealand. *Notornis,* **22,** 101-109.

Diamond, J.M. (1984) Distributions of New Zealand birds on real and virtual islands. *New Zealand Journal of Ecology,* **7,** 37-55.

Dijkgraaf, A.C. (2002) Phenology and frugivory of large-fruited species in Northern New Zealand and the impacts of introduced mammals. PhD thesis, University of Auckland, New Zealand.

Dormann, C.F., Gruber, B. & Frund, J. (2008) Introducing the bipartite package: analysing ecological networks. *R news,* **8,** 8-11.

Duncan, R.P. (1997) The role of competition and introduction effort in the success of passeriform birds introduced to New Zealand. *The American Naturalist,* **149,** 903-915.

Dungan, R.J., O'Cain, M.J., Lopez, M.L. & Norton, D.A. (2002) Contribution by possums to seed rain and subsequent seed germination in successional vegetation, Canterbury, New Zealand. *New Zealand Journal of Ecology,* **26,** 121-127.

Eckhardt, R.C. (1972) Introduced plants and animals in the Galápagos Islands. *Bioscience,* **22,** 585-590.

Emeny, M.T., Powlesland, R.G., Henderson, I.M. & Fordham, R.A. (2009) Feeding ecology of kereru (*Hemiphaga novaeseelandiae*) in podocarp-hardwood forest, Whirinaki Forest Park, New Zealand. *New Zealand Journal of Ecology,* **33,** 114-124.

Environment Canterbury (2008) Priceless Podocarps. *Living Here*. Christchurch, New Zealand.

Fitzgerald, A.E. (1977) Number and weight of faecal pellets produced by opossums. *Proceedings of the New Zealand Ecological Society,* **24,** 76-78.

Fitzsimons, M.S. & Miller, R.M. (2010) The importance of soil microorganisms for maintaining diverse plant communities in tallgrass prairie. *American Journal of Botany,* **97,** 1937-1943.

Fontaine, C., Collin, C.L. & Dajoz, I. (2008) Generalist foraging of pollinators: diet expansion at high density. *Journal of Ecology,* **96,** 1002-1010.

French, K., Odowd, D.J. & Lill, A. (1992) Fruit removal of *Coprosma quadrifida* (Rubiaceae) by birds in South-Eastern Australia. *Australian Journal of Ecology,* **17,** 35-42.

Fuentes, M. (1994) Diets of fruit-eating birds: what are the causes of interspecific differences? *Oecologia,* **97,** 134-142.

Galetti, M. *et al.* (2013) Functional extinction of birds drives rapid evolutionary changes in seed size. *Science,* **340,** 1086-1090.

García, C., Jordano, P. & Godoy, J.A. (2007) Contemporary pollen and seed dispersal in a *Prunus mahaleb* population: patterns in distance and direction. *Molecular Ecology,* **16,** 1947-1955.

Gibb, J.A. (1996) First seen or first heard? A useful distinction when counting forest birds. *Notornis,* **43,** 7-18.

Gibbs, G.W. (2006) *Ghosts of Gondwana: the history of life in New Zealand*. Craig Potton, Nelson, New Zealand.

Gotelli, N.J. & Colwell, R.K. (2001) Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters,* **4,** 379-391.

Graham, C.H., Moermond, T.C., Kristensen, K.A. & Mvukiyumwami, J. (1995) Seed dispersal effectiveness by two bulbuls on *Maesa lanceolata*, an African montane forest tree. *Biotropica,* **27,** 479-486.

Green, W. & Coleman, J. (1986) Movement of possums (*Trichosurus vulpecula*) between forest and pasture in Westland, New Zealand: implications for bovine tuberculosis transmission. *New Zealand Journal of Ecology,* **9,** 57-70.

Green, W.Q. (1984) A review of ecological studies relevant to management of the common brushtail possum. *Possums and gliders* (eds A. Smith & I.D. Hume), pp. 483-499. Surrey Beatty/Australian Mammal Society, Chipping Norton, Australia.

Hampe, A. (2003) Frugivory in European Laurel: how extinct seed dispersers have been substituted. *Bird Study,* **50,** 280-284.

Handel, S.N. (1997) The role of plant-animal mutualisms in the design and restoration of natural communities. *Restoration Ecology and Sustainable Development* (eds K.M. Urbanska, N.R. Webb & P.J. Edwards), pp. 111-132. Cambridge University Press, Cambridge, UK.

Heather, B.D. & Robertson, H.A. (2000) *The field guide to the birds of New Zealand,* Rev. edn. Viking, Auckland, New Zealand.

Herrera, C.M. (1984) A study of avian frugivores, bird-dispersed plants, and their interaction in mediterranean scrublands. *Ecological Monographs,* **54,** 2-23.

Herrera, C.M. (1998) Long-term dynamics of Mediterranean frugivorous birds and fleshy fruits: a 12-year study. *Ecological Monographs,* **68,** 511-538.

Herrera, C.M. (2002) Seed dispersal by vertebrates. *Plant-Animal Interactions: An Evolutionary Approach* (eds C.M. Herrera & O. Pellmyr), pp. 185-208. Blackwell Science, Oxford, UK.

Herrera, C.M., Jordano, P., Lopez-Soria, L. & Amat, J.A. (1994) Recruitment of a mast-fruiting, bird-dispersed tree: bridging frugivore activity and seedling establishment. *Ecological Monographs,* **64,** 315-344.

HilleRisLambers, J., Clark, J.S. & Beckage, B. (2002) Density-dependent mortality and the latitudinal gradient in species diversity. *Nature,* **417,** 732-735.

Holdaway, R. (1989) New Zealand's pre-human avifauna and its vulnerability. *New Zealand Journal of Ecology,* **12,** 11-25.

Holdaway, R.N. (1999) Introduced predators and avifaunal extinction in New Zealand. *Extinctions in Near Time: Causes, Contexts, and Consequences* (ed. D.E. MacPhee), pp. 189-238. KluwerAcademic/Plenum Publishers, New York.

Holthuijzen, A.M.A. & Adkisson, C.S. (1984) Passage rate, energetics, and utilization efficiency of the cedar waxwing. *The Wilson Bulletin,* **96,** 680-684.

Hoppes, W.G. (1988) Seedfall pattern of several species of bird-dispersed plants in an Illinois woodland. *Ecology,* **69,** 320-329.

Howe, H., Schupp, E.W. & Westley, L. (1985) Early consequences of seed dispersal for a neotropical tree (*Virola surinamensis*). *Ecology,* **66,** 781-791.

Howe, H.F. & Smallwood, J. (1982) Ecology of seed dispersal. *Annual Review of Ecology and Systematics,* **13,** 201-228.

Hunt, D.M. (1978) Kowhai Bush: a valuable remnant of lowland forest. *Forest and Bird,* **210,** 18-21.

Hurst, S.E., Turnbull, M.H. & Norton, D.A. (2002) The effect of plant light environment on mycorrhizal colonisation in field-grown seedlings of podocarp-angiosperm forest tree species. *New Zealand Journal of Botany,* **40,** 65-72.

Hurtt, G.C. & Pacala, S.W. (1995) The consequences of recruitment limitation: reconciling chance, history and competitive differences between plants. *Journal of Theoretical Biology,* **176,** 1-12.

Hyatt, L.A. *et al.* (2003) The distance dependence prediction of the Janzen-Connell hypothesis: a meta-analysis. *Oikos,* **103,** 590-602.

Iles, J.M. (2012) Is Maungatautari restoring bird pollination and seed dispersal services? MSc thesis, University of Canterbury, New Zealand.

Innes, J., Burns, B., Fitzgerald, N., Thornburrow, D. & Watts, C. (2003) Pre-mammal eradication bird counts at Maungatautari and Pirongia, November-December 2002. Landcare Research Contract Report 0203/095 to Foundation for Research, Science and Technology.

Innes, J., Hay, R., Flux, I., Bradfield, P., Speed, H. & Jansen, P. (1999) Successful recovery of North Island kokako *Callaeas cinerea wilsoni* populations, by adaptive management. *Biological Conservation,* **87,** 201-214.

Innes, J., Kelly, D., Overton, J.M. & Gillies, C. (2010) Predation and other factors currently limiting New Zealand forest birds. *New Zealand Journal of Ecology,* **34,** 86-114.

Innes, J., Nugent, G., Prime, K. & Spurr, E.B. (2004) Responses of kukupa (*Hemiphaga novaeseelandiae*) and other birds to mammal pest control at Motatau, Northland. *New Zealand Journal of Ecology,* **28,** 73-81.

Izhaki, I. (2002) The role of fruit traits in determining fruit removal in East Mediterranean ecosystems. *Seed Dispersal and Frugivory: Ecology, Evolution and Conservation* (eds D.J. Levey, W.R. Silva & M. Galetti), pp. 161-175. CABI, Wallingford, UK.

Jacobs, J. (1974) Quantitative measurement of food selection. *Oecologia,* **14,** 413-417.

Jana, R.C. (2012) Animal seed dispersal and its consequences for plant recruitment. PhD thesis, University of Canterbury, New Zealand.

Janzen, D.H. (1970) Herbivores and the number of tree species in tropical forests. *The American Naturalist,* **104,** 501-528.

Jordano, P. & Godoy, J.A. (2002) Frugivore-generated seed shadows: a landscape view of demographic and genetic effects. *Seed Dispersal and Frugivory: Ecology, Evolution and Conservation* (eds D.J. Levey, W.R. Silva & M. Galetti), pp. 305-321. CABI, Wallingford, UK.

Kawakami, K., Mizusawa, L. & Higuchi, H. (2009) Re-established mutualism in a seed-dispersal system consisting of native and introduced birds and plants on the Bonin Islands, Japan. *Ecological Research,* **24,** 741-748.

Kelly, D. *et al.* (2005) Can stoat (*Mustela erminea*) trapping increase bellbird (*Anthornis melanura*) populations and benefit mistletoe (*Peraxilla tetrapetala*) pollination? *New Zealand Journal of Ecology,* **29,** 69-82.

Kelly, D., Ladley, J.J. & Robertson, A.W. (2004) Is dispersal easier than pollination? Two tests in New Zealand Loranthaceae. *New Zealand Journal of Botany,* **42,** 89-103.

Kelly, D., Ladley, J.J., Robertson, A.W., Anderson, S.H., Wotton, D.M. & Wiser, S.K. (2010) Mutualisms with the wreckage of an avifauna: the status of bird pollination and fruit-dispersal in New Zealand. *New Zealand Journal of Ecology,* **34,** 66-85.

Kelly, D., Robertson, A.W., Ladley, J.J., Anderson, S.H. & McKenzie, R.J. (2006) The relative (un)importance of introduced animals as pollinators and dispersers of native plants. *Biological invasions in New Zealand* (eds R. Allen & W.G. Lee), pp. 227-245. Springer-Verlag, Berlin, Germany.

Kikkawa, J. (1966) Population distribution of land birds in temperate rainforest of southern New Zealand. *Transactions of the Royal Society of New Zealand,* **7,** 215-277.

Kitajima, K. & Augspurger, C.K. (1989) Seed and seedling ecology of a monocarpic tropical tree, *Tachigalia versicolor*. *Ecology,* **70,** 1102-1114.

Knowles, B. & Beveridge, A.E. (1982) Biological flora of New Zealand 9. *Beilschmiedia tawa* (a-Cunn) Benth Et Hook-F Ex Kirk (Lauraceae) Tawa. *New Zealand Journal of Botany,* **20,** 37-54.

Ladley, J.J. & Kelly, D. (1996) Dispersal, germination and survival of New Zealand mistletoes (Loranthaceae): dependence on birds. *New Zealand Journal of Ecology,* **20,** 69-79.

Laman, T.G. (1996) *Ficus* seed shadows in a Bornean rainforest. *Oecologia,* **107,** 347-355.

Lee, W.G., Clout, M.N., Robertson, H.A. & Wilson, J.B. (1991) Avian dispersers and fleshy fruits in New Zealand. *Acta XX Congressus Internationalis Ornithologici* (ed. M.J. Williams), pp. 1617-1623. New Zealand Ornithological Congress Trust Board, Wellington, New Zealand.

Lee, W.G., Wood, J.R. & Rogers, G.M. (2010) Legacy of avian-dominated plant-herbivore systems in New Zealand. *New Zealand Journal of Ecology,* **34,** 28-47.

Levey, D.J. & Karasov, W.H. (1994) Gut passage of insects by European starlings and comparison with other species. *The Auk,* **111,** 478-481.

Levin, S.A., Muller-Landau, H.C., Nathan, R. & Chave, J. (2003) The ecology and evolution of seed dispersal: a theoretical perspective. *Annual Review of Ecology Evolution and Systematics,* **34,** 575-604.

Levine, J.M. & Murrell, D.J. (2003) The community-level consequences of seed dispersal patterns. *Annual Review of Ecology Evolution and Systematics,* **34,** 549-574.

Lloyd, B. (2001) Advances in New Zealand mammalogy 1990-2000: Short-tailed bats. *Journal of the Royal Society of New Zealand,* **31,** 59-81.

Lord, J.M., Markey, A.S. & Marshall, J. (2002) Have frugivores influenced the evolution of fruit traits in New Zealand? *Seed Dispersal and Frugivory: Ecology, Evolution and Conservation* (eds D.J. Levey, W.R. Silva & M. Galetti), pp. 55-68. CABI, Wallingford, UK.

Lunn, D.J., Thomas, A., Best, N. & Spiegelhalter, D. (2000) WinBUGS - a Bayesian modelling framework: concepts, structure, and extensibility. *Statistics and Computing,* **10,** 325-337.

Macarthur, R.H. & Pianka, E.R. (1966) On optimal use of a patchy environment. *American Naturalist,* **100,** 603-609.

MacFarlane, A. (2012) Frugivorous mutualisms in a native New Zealand forest: the good the bad and the ugly. MSc thesis, University of Canterbury, New Zealand.

Martin, P.H. & Canham, C.D. (2010) Dispersal and recruitment limitation in native versus exotic tree species: life-history strategies and Janzen-Connell effects. *Oikos,* **119,** 807-824.

McConkey, K.R. & Drake, D.R. (2006) Flying foxes cease to function as seed dispersers long before they become rare. *Ecology,* **87,** 271-276.

McConkey, K.R., Prasad, S., Corlett, R.T., Campos-Arceiz, A., Brodie, J.F., Rogers, H. & Santamaria, L. (2012) Seed dispersal in changing landscapes. *Biological Conservation,* **146,** 1-13.

McEwen, W.M. (1978) The food of the New Zealand pigeon (*Hemiphaga novaeseelandiae novaeseelandiae*). *New Zealand Journal of Ecology,* **1,** 99-108.

McNutt, K.L. (1998) Impacts of reduced bird densities on pollination and dispersal mutualisms in New Zealand forests. MSc thesis, Massey University, New Zealand.

Meurk, C.D. & Swaffield, S.R. (2000) A landscape ecological framework for indigenous regeneration in rural New Zealand-Aotearoa. *Landscape and Urban Planning,* **50,** 129-144.

Miller, C. (2002) Conservation of riparian forest remnants, West Coast, New Zealand. *Landscape Research,* **27,** 125-140.

Miskelly, C.M. *et al.* (2008) Conservation status of New Zealand birds, 2008. *Notornis,* **55,** 117-135.

Moles, A.T. & Drake, D.R. (1999) Post-dispersal seed predation on eleven large-seeded species from the New Zealand flora: a preliminary study in secondary forest. *New Zealand Journal of Botany,* **37,** 679-685.

Montgomery, B.R., Kelly, D. & Ladley, J.J. (2001) Pollinator limitation of seed set in *Fuchsia perscandens* (Onagraceae) on Banks Peninsula, South Island, New Zealand. *New Zealand Journal of Botany,* **39,** 559-565.

Moors, P. (1983) Predation by mustelids and rodents on the eggs and chicks of native and introduced birds in Kowhai Bush, New Zealand. *Ibis,* **125,** 137-154.

Moran, C., Catterall, C.P. & Kanowski, J. (2009) Reduced dispersal of native plant species as a consequence of the reduced abundance of frugivore species in fragmented rainforest. *Biological Conservation,* **142,** 541-552.

Murphy, D.J. & Kelly, D. (2001) Scarce or distracted? Bellbird (*Anthornis melanura*) foraging and diet in an area of inadequate mistletoe pollination. *New Zealand Journal of Ecology,* **25,** 69-81.

Nathan, R. & Muller-Landau, H.C. (2000) Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends in Ecology & Evolution,* **15,** 278-285.

Norton, D. & Reid, N. (2013) *Nature and Farming: Sustaining Native Biodiversity in Agricultural Landscapes*. CSIRO, Collingwood, Australia.

NPCA (2010) *Possum population monitoring using the WaxTag® method*. National Possum Control Agencies, Wellington, New Zealand.

Nugent, G., Fraser, W. & Sweetapple, P. (2001) Top down or bottom up? Comparing the impacts of introduced arboreal possums and 'terrestrial' ruminants on native forests in New Zealand. *Biological Conservation,* **99,** 65-79.

Nugent, G., Sweetapple, P., Coleman, J. & Suisted, P. (2000) Possum feeding habits: dietary tactics of a reluctant folivore. *The brushtail possum: biology, impact and management of an introduced marsupial* (ed. T.L. Montague), pp. 10-23. Manaaki Whenua Press, Lincoln, New Zealand.

O'Brien, T.G., Kinnaird, M.F., Dierenfeld, E.S., Conklin-Brittain, N.L., Wrangham, R.W. & Silver, S.C. (1998) What's so special about figs? *Nature,* **392,** 668.

O'Connor, S.-J. (2006) Modelling seed dispersal by tui. BSc Honours thesis, University of Canterbury, New Zealand.

O'Connor, S.-J. (2012) Quantifying seed dispersal of matai (*Prumnopitys taxifolia*). PhD thesis, University of Canterbury, New Zealand.

O'Connor, S.-J. & Kelly, D. (2012) Seed dispersal of matai (*Prumnopitys taxifolia*) by feral pigs (*Sus scrofa*). *New Zealand Journal of Ecology,* **36,** 228-231.

O'Donnell, C.F. (1996) Predators and the decline of New Zealand forest birds: an introduction to the hole-nesting bird and predator programme. *New Zealand Journal of Zoology,* **23,** 213-219.

O'Donnell, C.F. & Hoare, J.M. (2012) Quantifying the benefits of long-term integrated pest control for forest bird populations in a New Zealand temperate rainforest. *New Zealand Journal of Ecology,* **36,** 131-140.

O'Donnell, C.F.K. & Dilks, P.J. (1994) Foods and foraging of forest birds in temperate rainforest, South Westland, New Zealand. *New Zealand Journal of Ecology,* **18,** 87-107.

Olson, S.L. (1989) Extinction on islands: man as a catastrophe. *Conservation for the twenty-first century* (eds D. Western & M.C. Pearl), pp. 50-53. Oxford University Press, Oxford, UK.

Packer, A. & Clay, K. (2000) Soil pathogens and spatial patterns of seedling mortality in a temperate tree. *Nature,* **404,** 278-281.

Parker, J.D., Burkepile, D.E. & Hay, M.E. (2006) Opposing effects of native and exotic herbivores on plant invasions. *Science,* **311,** 1459-1461.

Paterson, B.M., Morris, R.S., Weston, J. & Cowan, P.E. (1995) Foraging and denning patterns of brushtail possums, and their possible relationship to contact with cattle and the transmission of bovine tuberculosis. *New Zealand Veterinary Journal,* **43,** 281-288.

Poole, A.L. & Adams, N.M. (1994) *Trees and shrubs of New Zealand,* Rev. edn. Manaaki Whenua Press, Lincoln, New Zealand.

Poulsen, J.R., Clark, C.J. & Smith, T.B. (2001) Seed dispersal by a diurnal primate community in the Dja Reserve, Cameroon. *Journal of Tropical Ecology,* **17,** 787-808.

Pracy, L.T. (1974) *Introduction and liberation of the opossum (Trichosurus vulpecula) into New Zealand,* 2nd edn. New Zealand Forest Service, Wellington, New Zealand.

Redford, K.H. & Feinsinger, P. (2001) The half-empty forest: sustainable use and the ecology of interactions. *Conservation of exploited species* (eds J. Reynolds, G. Mace, K. Redford & J. Robinson), pp. 370-399. Cambridge University Press, Cambridge, UK.

Ribbens, E., Silander Jr, J.A. & Pacala, S.W. (1994) Seedling recruitment in forests: calibrating models to predict patterns of tree seedling dispersion. *Ecology,* **75,** 1794-1806.

Richard, Y. & Armstrong, D.P. (2010) Cost distance modelling of landscape connectivity and gap-crossing ability using radio-tracking data. *Journal of Applied Ecology,* **47,** 603-610.

Riera, N., Traveset, A. & García, O. (2002) Breakage of mutualisms by exotic species: the case of *Cneorum tricoccon* L. in the Balearic Islands (Western Mediterranean Sea). *Journal of Biogeography,* **29,** 713-719.

Robertson, A.W., Kelly, D. & Ladley, J.J. (2011) Futile selfing in the trees *Fuchsia excorticata* (Onagraceae) and *Sophora microphylla* (Fabaceae): inbreeding depression over 11 years. *International Journal of Plant Sciences,* **172,** 191-198.

Robertson, A.W., Ladley, J.J., Kelly, D., McNutt, K.L., Peterson, P.G., Merrett, M.F. & Karl, B.J. (2008) Assessing pollination and fruit dispersal in *Fuchsia excorticata* (Onagraceae). *New Zealand Journal of Botany,* **46,** 299-314.

Robertson, A.W., Trass, A., Ladley, J.J. & Kelly, D. (2006) Assessing the benefits of frugivory for seed germination: the importance of the deinhibition effect. *Functional Ecology,* **20,** 58-66.

Robertson, C., Hyvönen, P., Fraser, M. & Pickard, C. (2007) *Atlas of bird distribution in New Zealand 1999-2004*. The Ornithological Society of New Zealand, Wellington, New Zealand.

Roff, D.A. & Roff, R.J. (2003) Of rats and Maoris: a novel method for the analysis of patterns of extinction in the New Zealand avifauna before European contact. *Evolutionary Ecology Research,* **5,** 759-779.

Ruscoe, W.A., Wilson, D., McElrea, L., McElrea, G. & Richardson, S.J. (2004) A house mouse (*Mus musculus*) population eruption in response to rimu (*Dacrydium cupressinum*) seedfall in southern New Zealand. *New Zealand Journal of Ecology,* **28,** 259-265.

Saba, S.L. & Toyos, A. (2003) Seed removal by birds, rodents and ants in the Austral portion of the Monte Desert, Argentina. *Journal of Arid Environments,* **53,** 115-124.

Schaefer, H.M., Schmidt, V. & Bairlein, F. (2003a) Discrimination abilities for nutrients: which difference matters for choosy birds and why? *Animal Behaviour,* **65,** 531-541.

Schaefer, H.M., Schmidt, V. & Winkler, H. (2003b) Testing the defence trade-off hypothesis: how contents of nutrients and secondary compounds affect fruit removal. *Oikos,* **102,** 318-328.

Schipper, J. *et al.* (2008) The status of the world's land and marine mammals: diversity, threat, and knowledge. *Science,* **322,** 225-230.

Schupp, E.W. (1992) The Janzen-Connell model for tropical tree diversity: population implications and the importance of spatial scale. *American Naturalist,* **140,** 526-530.

Schupp, E.W. (1993) Quantity, quality and the effectiveness of seed dispersal by animals. *Vegetatio,* **107/108,** 15-29.

Schupp, E.W. & Fuentes, M. (1995) Spatial patterns of seed dispersal and the unification of plant-population ecology. *Ecoscience,* **2,** 267-275.

Schupp, E.W., Milleron, T. & Russo, S.E. (2002) Dissemination limitation and the origin and maintenance of species-rich tropical forests. *Seed Dispersal and Frugivory: Ecology, Evolution and Conservation* (eds D.J. Levey, W.R. Silva & M. Galetti), pp. 19-33. CABI, Wallingford, UK.

Scofield, D.G. & Schultz, S.T. (2006) Mitosis, stature and evolution of plant mating systems: low-Phi and high-Phi plants. *Proceedings of the Royal Society - Series B: Biological Sciences,* **273,** 275-282.

Sekercioglu, C.H., Daily, G.C. & Ehrlich, P.R. (2004) Ecosystem consequences of bird declines. *Proceedings of the National Academy of Sciences of the United States of America,* **101,** 18042-18047.

Sethi, P. & Howe, H.F. (2009) Recruitment of hornbill-dispersed trees in hunted and logged forests of the Indian Eastern Himalaya. *Conservation Biology,* **23,** 710-718.

Sharam, G.J., Sinclair, A. & Turkington, R. (2009) Serengeti birds maintain forests by inhibiting seed predators. *Science,* **325,** 51-51.

Sodhi, N.S., Koh, L.P., Brook, B.W. & Ng, P.K.L. (2004) Southeast Asian biodiversity: an impending disaster. *Trends in Ecology & Evolution,* **19,** 654-660.

Sorensen, A.E. (1984) Nutrition, energy and passage time: experiments with fruit preference in European blackbirds (*Turdus merula*). *Journal of Animal Ecology,* **53,** 545-557.

Sork, V.L. & Smouse, P.E. (2006) Genetic analysis of landscape connectivity in tree populations. *Landscape Ecology,* **21,** 821-836.

Spiegelhalter, D.J., Best, N.G., Carlin, B.P. & Van Der Linde, A. (2002) Bayesian measures of model complexity and fit. *Journal of the Royal Statistical Society: Series B (Statistical Methodology),* **64,** 583-639.

Staddon, S., Compton, S. & Portch, A. (2010) Dispersal of fig seeds in the Cook Islands: introduced frugivores are no substitutes for natives. *Biodiversity and Conservation,* **19,** 1905-1916.

Stanley, M.C. & Lill, A. (2002) Avian fruit consumption and seed dispersal in a temperate Australian woodland. *Austral Ecology,* **27,** 137-148.

Starling-Windhof, A., Massaro, M. & Briskie, J. (2011) Differential effects of exotic predator-control on nest success of native and introduced birds in New Zealand. *Biological Invasions,* **13,** 1021-1028.

Steadman, D.W. (2006) *Extinction and biogeography of tropical Pacific birds*. University of Chicago Press, Chicago.

Stewart, A.M. & Craig, J.L. (1985) Movements, status, access to nectar, and spatial organisation of the tui. *New Zealand Journal of Zoology,* **12,** 664-666.

Stoner, K.E. & Henry, M. (2008) Seed dispersal and frugivory in tropical ecosystems. *Encyclopedia of life support systems*. Eolss Publishers, Oxford, UK.

Sullivan, J.J., Burrows, C.J. & Dugdale, J.S. (1995) Insect predation of seeds of native New Zealand woody plants in some central South Island localities. *New Zealand Journal of Botany,* **33,** 355-364.

Sweetapple, P., Fraser, K. & Knightbridge, P. (2004) Diet and impacts of brushtail possum populations across an invasion front in South Westland, New Zealand. *New Zealand Journal of Ecology,* **28,** 19-33.

Temple, S.A. (1977) Plant-animal mutualism: coevolution with dodo leads to near extinction of plant. *Science,* **197,** 885-886.

Tennyson, A.J.D. (2010) The origin and history of New Zealand's terrestrial vertebrates. *New Zealand Journal of Ecology,* **34,** 6-27.

Terborgh, J. (2012) Enemies maintain hyperdiverse tropical forests. *The American Naturalist,* **179,** 303-314.

Terborgh, J. *et al.* (2008) Tree recruitment in an empty forest. *Ecology,* **89,** 1757-1768.

Thery, M. (1989) Consommation des fruits et dissémination des graines par le merle noir (*Turdus merula* L.) en zone périurbaine sous climat tempéré. *Acta oecologica. Oecologia applicata,* **10,** 271-285.

Thomas, M.D., Morgan, D.R. & Maddigan, F. (2007) Accuracy of possum monitoring using WaxTags (Pest Control Research Contract Report: 2007/7). Animal Health Board, New Zealand.

Thorsen, M.J., Dickinson, K.J.M. & Seddon, P.J. (2009) Seed dispersal systems in the New Zealand flora. *Perspectives in Plant Ecology Evolution and Systematics,* **11,** 285-309.

Towns, D.R., Atkinson, I.A. & Daugherty, C.H. (2006) Have the harmful effects of introduced rats on islands been exaggerated? *Biological Invasions,* **8,** 863-891.

Traveset, A. (1998) Effect of seed passage through vertebrate frugivores' guts on germination: a review. *Perspectives in Plant ecology, evolution and systematics,* **1,** 151-190.

Traveset, A., Bermejo, T. & Willson, M. (2001) Effect of manure composition on seedling emergence and growth of two common shrub species of Southeast Alaska. *Plant Ecology,* **155,** 29-34.

Traveset, A., González-Varo, J.P. & Valido, A. (2012) Long-term demographic consequences of a seed dispersal disruption. *Proceedings of the Royal Society B: Biological Sciences,* **279,** 3298-3303.

Traveset, A. & Richardson, D.M. (2006) Biological invasions as disruptors of plant reproductive mutualisms. *Trends in Ecology & Evolution,* **21,** 208-216.

Traveset, A., Robertson, A.W. & Rodriguez-Perez, J. (2007) A review on the role of endozoochory in seed germination. *Seed Dispersal: Theory and its Application in a Changing World* (eds A.J. Dennis, E.W. Schupp, R.J. Green & D.A. Westcott), pp. 78-103. CABI, Wallingford, UK.

Traveset, A. & Verdu, M. (2002) A meta-analysis of the effect of gut treatment on seed germination. *Seed Dispersal and Frugivory: Ecology, Evolution and Conservation* (eds D.J. Levey, W.R. Silva & M. Galetti), pp. 339-350. CABI, Wallingford, UK.

Vanthomme, H., Bellé, B. & Forget, P.M. (2010) Bushmeat hunting alters recruitment of large-seeded plant species in central Africa. *Biotropica,* **42,** 672-679.

Verdu, M. & Traveset, A. (2004) Bridging meta-analysis and the comparative method: a test of seed size effect on germination after frugivores' gut passage. *Oecologia,* **138,** 414-418.

Vilà, M. & Sardans, J. (1999) Plant competition in mediterranean-type vegetation. *Journal of Vegetation Science,* **10,** 281-294.

Vitousek, P.M., D'Antonio, C.M., Loope, L.L., Rejmanek, M. & Westbrooks, R. (1997) Introduced species: a significant component of human-caused global change. *New Zealand Journal of Ecology,* **21,** 1-16.

Vitousek, P.M., Loope, L.L. & Stone, C.P. (1987) Introduced species in Hawaii: biological effects and opportunities for ecological research. *Trends in Ecology & Evolution,* **2,** 224-227.

Wenny, D.G. (2000) Seed dispersal, seed predation, and seedling recruitment of a neotropical montane tree. *Ecological Monographs,* **70,** 331-351.

Wenny, D.G., Devault, T.L., Johnson, M.D., Kelly, D., Sekercioglu, C.H., Tomback, D.F. & Whelan, C.J. (2011) The need to quantify ecosystem services provided by birds. *The Auk,* **128,** 1-14.

Westcott, D.A. (2007) Seed and seedling shadows. *Seed Dispersal: Theory and its Application in a Changing World* (eds A.J. Dennis, E.W. Schupp, R. Green & D.A. Westcott), pp. 197-199. CABI, Wallingford, UK.

Wheelwright, N.T. & Orians, G.H. (1982) Seed dispersal by animals: contrasts with pollen dispersal, problems of terminology, and constraints on coevolution. *American Naturalist,* **119,** 402-413.

Whelan, C.J., Wenny, D.G. & Marquise, R.J. (2008) Ecosystem services provided by birds. *Annals of the New York Academy of Sciences,* **1134,** 25-60.

Whitaker, A. (1987) The roles of lizards in New Zealand plant reproductive strategies. *New Zealand Journal of Botany,* **25,** 315-328.

Whitaker, A.H. (1972) An improved mist net rig for use in forests. *Bird-Banding,* **43,** 1-8.

Williams, K. (2005) *Native plant communities of the Canterbury Plains*. Department of Conservation, Christchurch, New Zealand.

Williams, P.A. (2003) Are possums important dispersers of large-seeded fruit? *New Zealand Journal of Ecology,* **27,** 221-223.

Williams, P.A. (2006) The role of blackbirds (*Turdus merula*) in weed invasion in New Zealand. *New Zealand Journal of Ecology,* **30,** 285-291.

Williams, P.A. & Buxton, R.P. (1986) Hawthorn (*Crataegus monogyna*) populations in mid-Canterbury. *New Zealand Journal of Ecology,* **9,** 11-17.

Williams, P.A. & Karl, B.J. (1996) Fleshy fruits of indigenous and adventive plants in the diet of birds in forest remnants, Nelson, New Zealand. *New Zealand Journal of Ecology,* **20,** 127-145.

Williams, P.A., Karl, B.J., Bannister, P. & Lee, W.G. (2000) Small mammals as potential seed dispersers in New Zealand. *Austral Ecology,* **25,** 523-532.

Wilmshurst, J.M., Anderson, A.J., Higham, T.F. & Worthy, T.H. (2008) Dating the late prehistoric dispersal of Polynesians to New Zealand using the commensal Pacific rat. *Proceedings of the National Academy of Sciences,* **105,** 7676-7680.

Wilson, D.J., Lee, W.G., Webster, R.A. & Allen, R.B. (2003) Effects of possums and rats on seedling establishment at two forest sites in New Zealand. *New Zealand Journal of Ecology,* **27,** 147-155.

Wilson, D.J., Ruscoe, W.A., Buffows, L.E., McElrea, L.M. & Choquenot, D. (2006) An experimental study of the impacts of understorey forest vegetation and herbivory by red deer and rodents on seedling establishment and species composition in Waitutu Forest, New Zealand. *New Zealand Journal of Ecology,* **30,** 191-207.

Wilson, D.J., Wright, E.F., Canham, C.D. & Ruscoe, W.A. (2007) Neighbourhood analyses of tree seed predation by introduced rodents in a New Zealand temperate rainforest. *Ecography,* **30,** 105-119.

Wilton, A.D. & Breitwieser, A.D. (2000) Composition of the New Zealand seed plant flora. *New Zealand Journal of Botany,* **38,** 537-549.

Wood, J.R. (2007) Moa gizzard content analyses: further information on the diets of *Dinornis robustus* and *Emeus crassus*, and the first evidence for the diet of *Pachyornis elephantopus* (Aves: Dinornithiformes). *Records of the Canterbury Museum,* **21,** 27-39.

Wotton, D.M. (2007) Consequences of dispersal failure: kereru and large seeds in New Zealand. PhD thesis, University of Canterbury, New Zealand.

Wotton, D.M., Clout, M.N. & Kelly, D. (2008) Seed retention times in the New Zealand pigeon (Hemiphaga novaezeelandiae novaeseelandiae). *New Zealand Journal of Ecology,* **32,** 1-6.

Wotton, D.M. & Kelly, D. (2011) Frugivore loss limits recruitment of large-seeded trees. *Proceedings of the Royal Society B: Biological Sciences,* **278,** 3345-3354.

Wotton, D.M. & Kelly, D. (2012) Do larger frugivores move seeds further? Body size, seed dispersal distance, and a case study of a large, sedentary pigeon. *Journal of Biogeography,* **39,** 1973-1983.

Wotton, D.M. & Ladley, J.J. (2008) Fruit size preference in the New Zealand pigeon (*Hemiphaga novaeseelandiae*). *Austral Ecology,* **33,** 341-347.

Wright, J.S. (2002) Plant diversity in tropical forests: a review of mechanisms of species coexistence. *Oecologia,* **130,** 1-14.

Wright, S.J. *et al.* (2007) The plight of large animals in tropical forests and the consequences for plant regeneration. *Biotropica,* **39,** 289-291.

Wyman, T.E., Trewick, S.A., Morgan-Richards, M. & Noble, A.D.L. (2011) Mutualism or opportunism? Tree fuchsia (*Fuchsia excorticata*) and tree weta (*Hemideina*) interactions. *Austral Ecology,* **36,** 261-268.

Yoshikawa, T. & Isagi, Y. (2012) Dietary breadth of frugivorous birds in relation to their feeding strategies in the lowland forests of central Honshu, Japan. *Oikos,* **121,** 1041-1052.

Young, L. (2012) Seed dispersal mutualisms and plant regeneration in New Zealand alpine ecosystems. PhD thesis, University of Canterbury, New Zealand.